KU LEUVEN

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Influence of wild boar (*Sus scrofa* L.) on vegetation development in the Meerdaal forest

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“The student declares that the submitted thesis text (including graphs) is original work, written using the wording of the student and reflecting the student’s English language proficiency. The text acknowledges, to the best of the ability and knowledge of the student, previous ideas and data.”

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Summary

The wild boar is a native ungulate species for Flanders, however due to overhunting and a reduction of forested area in the last centuries wild boar disappeared. After several decades of absence, wild boar officially reappeared in Flanders (Limburg) in 2006. Since then, a strong increase in both numbers and distribution has occurred, similar quick expansions are reported in many other countries. Due to these recent increases, the management and monitoring of wild boar has become an issue of global conservation concern. Wild boars are true ecosystem engineers, they can vastly influence species abundances, richness and ecosystem dynamics. Especially their typical rooting behavior can create ecosystem level effects. Studies on the impacts of wild boar on fauna and flora suggest density-dependent effects, this is in line with the intermediate disturbance hypothesis.

However, the environmental effects of wild boar are controversial, assessing impacts on natural systems is not straightforward. Wild boar can especially play an important role on forest ecosystems. They are probably the most important natural modifiers of plant communities.

At the moment there are limited numbers of good quantitative studies on the impacts of wild boar on forest biodiversity. Therefore, there is need for additional research. The most suitable ecosystem component for wild boars in temperate forests is the understory vegetation. This component is also a very important part of the forest overall biodiversity, accounting for up to 80% of plant species. Our aim is to contribute knowledge on the impacts of wild boar rooting in temperate forest. Our goals can be divided in two parts:

1) Non-temporal part: examining the relation between specific habitat parameters, plant functional traits and plant species and wild boar rooting intensity
2) Temporal part: Examining the impacts of wild boar recolonization and different levels of rooting intensity on understory vegetation development.

For two strict forest reserve in the Meerdaal forest, detailed vegetation relevés, soil and dendrometric data from three snapshots with different levels of wild boar density are available. For the last survey also detailed estimations of wild boar rooting distribution is available.

Our results suggest that wild boar prefer the forest stands with richer soils and plant communities. The presence of ancient woodland species seems to play an important role. Further, we can conclude that at the moment wild boar density is not high enough to delineate impacts, either positive or negative, exerted by wild boar. Are results are in line with a suggested shift towards a more mesic lowland oak and beech forest observed for these forest reserves, without current impact of wild boar.

Species introduction and impacts

Species introduction

Wild boar (*Sus scrofa*)

The wild boar (*Sus scrofa* Linnaeus, 1758), also known as wild hog, wild pig, feral swine, feral pig or feral hog, is a member of the Suidae family (Brunet et al., 2016; Ruvinsky & Rothschild, 1998). The Suidae are biologically seen quite monotypic, the representatives are omnivorous with a mostly herbivorous diet (Geptner et al., 1988). They exhibit a preference for different types of forests, steppes and forest steppes. The wild boar is the wild ancestor of the domestic pig, therefore all domestic pigs, feral pigs and their hybrids carry the same binominal name, *Sus scrofa* (Ruvinsky & Rothschild, 1998; T Scheppers & J Casaer, 2012). Animals younger than one year of age are called sucklings. Wild boars of age one until two are juveniles. From the 3 age they are called adults. Adult females are called sows and adult males are called boars (Geptner et al., 1988).

1 Distribution

1.1 Origin and global distribution

The genus *Sus* appeared some five million years ago in Eurasia during the early Pliocene (5.332 – 3.600 Ma) (Groenen et al., 2012; Meijaard et al., 2011). Later an expansion to North Africa occurred during the Pleistocene. The distribution in Africa remained limited to the highlands north of the Sahara Desert. Since no direct ancestor of *Sus* is known from Europe, it is assumed that they have colonized Europe through dispersal from Eastern Asia. It is suggested that the origin of this genus lies somewhere in the Philippines, the Malay Peninsula, Borneo, Java, or Sumatra. The ancestral population of *Sus* split in two groups. One group consisting of the Philippine Warty Pig (*S. philippensis*), the Visayan Warty Pig (*S. cebifrons*) and Mindoro Warty Pig *(S. oliveri*) now lives in the Philippines. The other group contains the pig species of mainland Asia, the western Malay Archipelago and Europe. However, much remains unclear, resulting in the need to resolve the taxonomy and phylogenetic position of many Suidae genera and species (Meijaard et al., 2011; Ruvinsky & Rothschild, 1998).

The Eurasian Wild Pig, *Sus scrofa* L., has the largest distribution of all naturally occurring wild pigs. It has even one of the largest distributions of all mammalian species (Ruvinsky & Rothschild, 1998). This large geographic range is reflected in a significant size and morphological variability of this species (Albarella et al., 2009). In the past, many of the more distinctive regional forms were described as full species. In later taxonomic reviews it was found that Sus scrofa formed a stepped cline extending from the Far East and South-East Asia to Western Europe (Kelm, 1939). This gradual shift in morphological characteristics allowed the combination of these different forms into one species (Meijaard et al., 2011). Thus, the species *Sus scrofa* is characterized by great genetic and geographic variation. Anthropogenic interferences through deliberate and accidental releases of domesticated, hybrid and pure-bred variants has further influenced this genetic and geographic variation (Meijaard et al., 2011). This great variability has been comprehensively examined, resulting in various assessments of the species systematics (Albarella et al., 2009). This led again to proposals of the separation of *S. scrofa* into different subspecies (among others: (Epstein, 1971; Genov, 1999; Groves, 1981; Mayer & Brisbin Jr, 1991). The number of subspecies found in literature varies between 4 and 25, depends on the definition given to the subspecies and is often ambiguous (Meijaard et al., 2011; Ruvinsky & Rothschild, 1998). For example, a very comprehensive review proposed the acceptance of 16 morphologically distinct populations. This work was based on craniometric and external characteristics (Groves, 1981; Groves & Grubb, 1993). Genov (1999) carried out similar craniometric analyses but proposed only the recognition of four subspecies. These analyses, however, did not incorporated some of the most distinct populations (Meijaard et al., 2011). Despite that, Genov (1999) merged these proposed subspecies into four widely geographic groupings, broadly embodying the more comprehensive review of Groves(Groves, 1981; Groves & Grubb, 1993).

According to Groves (1981; 1993), the subspecies *Sus scrofa scrofa* (L. 1758) represents the wild boars present in Western Europe. The distribution of this subspecies ranges from Poland, Czech Republic, Denmark and Germany to North Italy and the North Iberian Peninsula. The taxonomic status of animals living in Sweden, Finland, the Baltic states, Austria, Slovakia and Slovenia are unclear. Presumably these populations are included in *Sus scrofa scrofa* as well. Past restocking of depleted populations and reintroductions may have led to the introduction and mixing with other subspecies. For example in Italy, mixing may have occured with the *Sus scrofa attila* subspecies present in Hungary, Belarus, Ukraine, Moldova and southern Russia (Groves & Grubb, 1993; Meijaard et al., 2011).

Originally, the wild boar distribution was widespread. As we can see on figure 1 (Barrios-Garcia & Ballari, 2012), the western border of its native distribution were the British Isles. This western border included Ireland (Woodman et al., 1997) (not on the figure). Scandinavia and Southern Siberia formed the northern border. The eastern boundaries were Korea and Japan. The southern limits laid North of the Sahara and continued along the Nile Valley until Khartoum in Africa. Further following the continental coasts of East, South and South-east Asia. Within this vast range it was absent in some alpine zones like the high altitudes of Tien Shan and Pamir and in the driest deserts like some regions in China and Mongolia (Meijaard et al., 2011; Oliver, 1993; Ruvinsky & Rothschild, 1998; Sjarmidi & Gerard, 1988).

Figure 1: Distribution map wild boar. Black: native range, gray: introduced, circles: islands with introduced wild boar and "?": occurrence but unknown local distribution (Barrios-Garcia & Ballari, 2012)

In the past recent centuries, human overexploitation and changes in available habitat led to a drastic reduction in their distribution and numbers (Apollonio et al., 2010; Apollonio et al., 1988; Linnell & Zachos, 2010; Meijaard et al., 2011; Veličković et al., 2016). For example, up until the 12th century the species may have been present in Ireland, in the 16th they disappeared from Great Britain, in Sweden they were hunted to extinction in the 17th century, and during the 19th century they disappeared from Denmark. Furthermore, their range and abundance were greatly reduced in the 20th century in areas like Germany, Russia, Sudan and Tunisia (Harting, 1880; McCormick & Murray, 2011; Meijaard et al., 2011; Oliver, 1993; Thurfjell et al., 2009).

After these severe declines, there were some small recoveries in Russia, Spain, Germany, and Italy in the mid-20th century (Meijaard et al., 2011). A remarkable increase in wild boar populations and range has been recorded since the past 4-5 decades. An example is given by Pfaff and Saint Andrieux (2007): less than 100,000 boars were shot in the late 1980s in France, more recent counts of shot wild boar in 2002 reached up to 450,000 individuals. Comparable trends are observed in many other European countries and other parts of the world. This increase is related with various socio-economic and ecological changes like; the lack of large predators due to overhunting, deliberate releases for hunting, supplementary feeding, more frequent mast years and milder winters due to climate change, depopulation and abandonment of rural land, changes in agricultural practices, re-naturalization of wild boar habitats, decreased hunting across Europe, and their high reproductive rates (Apollonio et al., 2010; Ferreira et al., 2009; Fonseca, 2004; Massei & Genov, 2004; Massei et al., 2015; Massei et al., 2011; Scandura et al., 2011; Sáaez-Royuela & Telleriia, 1986; Tack, 2018; Touzot et al., 2020; Valente et al., 2020; Veličković et al., 2016). Due to this, assisted and natural range expansions occurred for example in Finland, Sweden and Estonia (Erkinaro, 1982). The presence in Sweden led to the recolonization of Norway where the first wild boar after local extinction was shot in 2013 (Rosvold & Andersen, 2008). The wild boar has also been inadvertently reintroduced in some countries. For example, in the United Kingdom and in Denmark the wild boar has become reestablished via escapes from commercial farming (Andersen & Holthe, 2010; Meijaard et al., 2011; Wilson, 2005; Wilson, 2013). The first new sighting of wild boar in Ireland dates from 2009, the exact mechanism of reestablishment in

Ireland is unknown. Both farm escapes and/or illegal releases are suspected (McDevitt et al., 2013). Nowadays, they also occur as introduced exotic populations in various parts of the world including New Zealand, Australia, North, Central and South America. Often in these non-native areas they are recognized as pest species (Barrios-Garcia & Ballari, 2012; Meijaard et al., 2011). Their omnivorous diet and capacity to live in different climatic conditions is an important feature contributing to this wide distribution (Ruvinsky & Rothschild, 1998).

1.2 Distribution in Belgium

To describe the past and present distribution of ungulates in Belgium, a distinction between Flanders and Wallonia should be made. These parts vary for example in terms of human populations density and forest cover. These factors influence the wild boar distribution and density significantly. For example, in 2020 the Walloon region had an average human population density of 216 inhabitants per square kilometer, the Flemish region has a density of 487 inhabitants per square kilometer (https://statbel.fgov.be/). According to a forest assessment between 2009 and 2019 the Flemish region has 140.279 ha of forest, merely 10% of the entire Flemish region(ANB, 1997-1999, 2009-2019). With 554.000 ha forest, around a third of the Walloon region is covered with forest (SRFB, n.d.). Since 1980, these two regions also have their own hunting laws, organizations, and seasons (Casaer & Licoppe, 2010)

Up until the end of the eighteenth-century wild boar was present in both Wallonia and Flanders. They presumably occurred in high densities in the larger forested areas around Leuven, South of Brussels and in the Ardennes (Casaer & Licoppe, 2010). To reduce damage in agricultural fields and in forests, emperor Joseph II installed an act at the end of this eighteenth-century (1781). He prohibited the free roaming of wild boar in the Southern Netherlands and ordered the killing or capture the overabundant wild boar populations (Baeté, 2011; Baeté et al., 2009). This order led to a first decrease in wild boar, and other ungulate species, populations. The populations of wild boar in the Belgian forests got further reduced by the various wars and revolutions since the end of the eighteenth century (Casaer & Licoppe, 2010).

Due to such a war beginning in 1792, current Belgium fell under French rule after the victory of France at Fleurus in June 1794 (Rapport, 2002). The French Revolution led to the abolishment of the aristocratic privilege of hunting, every citizen was now allowed to hunt. The democratization of hunting practices led to further decimation of most ungulate species and widespread damages to forest ecosystems (Estève, 2004). With the independence of Belgium in 1830, actions were done to restore our wildlife populations. Deer species were reintroduced at several places and a new hunting law was installed. These actions led to an increase of population size and distribution of ungulate species (Casaer & Licoppe, 2010). But later, the two World Wars in the twentieth century led again to a drastic reduction in wildlife populations. These wars led to a reduction of forested areas, increased poaching, and less control by authorities. After World War II wild boar populations started booming again in Wallonia, but not in Flanders (Casaer & Licoppe, 2010).

Using hunting bag data gathered during the last few a clear increase in wild boar numbers was found for Wallonia (figure 2). In this study data from Flanders was not included since wild boar recolonized Flanders only recently (Massei et al., 2014).

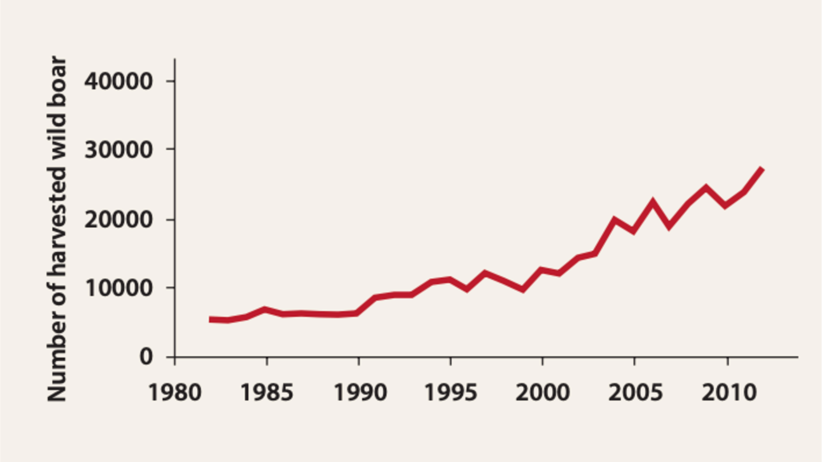


Figure 2: Trend in wild boar count in hunting bags in Belgium (Wallonia) (Tack, 2018), adapted from Massei et al. (2014)

In Flanders wild boar was ubiquitous until the eighteenth century. Later, up until the twentieth century, there were only irregular sightings of wandering individuals and sounders from Wallonia (Casaer & Van Den Berge, 2006; Tack et al., 1993; Van Herzele et al., 2015). After the second world war, wild boar disappeared from Flanders due to overhunting and eradication to reduce agricultural damage (Geeraerts et al., 2019; Rutten et al., 2019a; Rutten et al., 2019; Rutten et al., 2019c). Only in Voeren, a small and fairly permanent population got reestablished via migration (Mercelis, 2003; Volckaert & Verheyen, 2013). Voeren is situated South of the Meuse River and thus separated from the rest of Flanders (Geeraerts et al., 2019). This core is connected to a larger population in the province of Liège and other adjacent populations in the Netherlands and Germany. In the last decades of the twentieth century several sightings of wild boar were reported in other parts of Flanders. When these sightings were indeed of wild boar, these were always sightings of escaped animals (Casaer & Van Den Berge, 2006). The first observations of wild boar in the twenty-first century were made in 2005-2006 in the area around Zedelgem (vicinity of Bruges). In 2006 first sightings were recorded in the “Vallei van de Zwarte Beek” and Meerdaal Forest, in 2007 in the Sonian Forest and in 2008 in Averbode (Casaer, 2008).

After several decades of absence (Voeren not considered), in 2006 wild boar officially reappeared in Limburg. Founder populations were found in two geographically distinct areas, these populations were geographically not connected to already existing populations. Therefore, natural recolonization by migration can be excluded. There is no evidence on the source of these founder populations (Rutten et al., 2019a; Rutten et al., 2019c). The first reported shot wild boar outside Voeren also dates from 2006, namely in the vicinity of Bruges

(Zedelgem) (Geeraerts et al., 2019; Thomas Scheppers & Jim Casaer, 2012). Figure 3 gives the number of shot animals in Flanders per province and for Voeren between 2006 and 2020. The number of hunted wild boar in Flanders has increased since its return, with the lion's share in the province of Limburg (figure 3). In 2006 only 1 individual was reported while in 2020 more than 2300 individuals were counted in hunting bags. Between 2012 and 2015 the numbers of shot animals were stable, but since 2016 we see an almost exponential. Although it is impossible to determine the exact number of wild boars, estimates based on the culling data are important to gain insight into estimates like the minimum population.

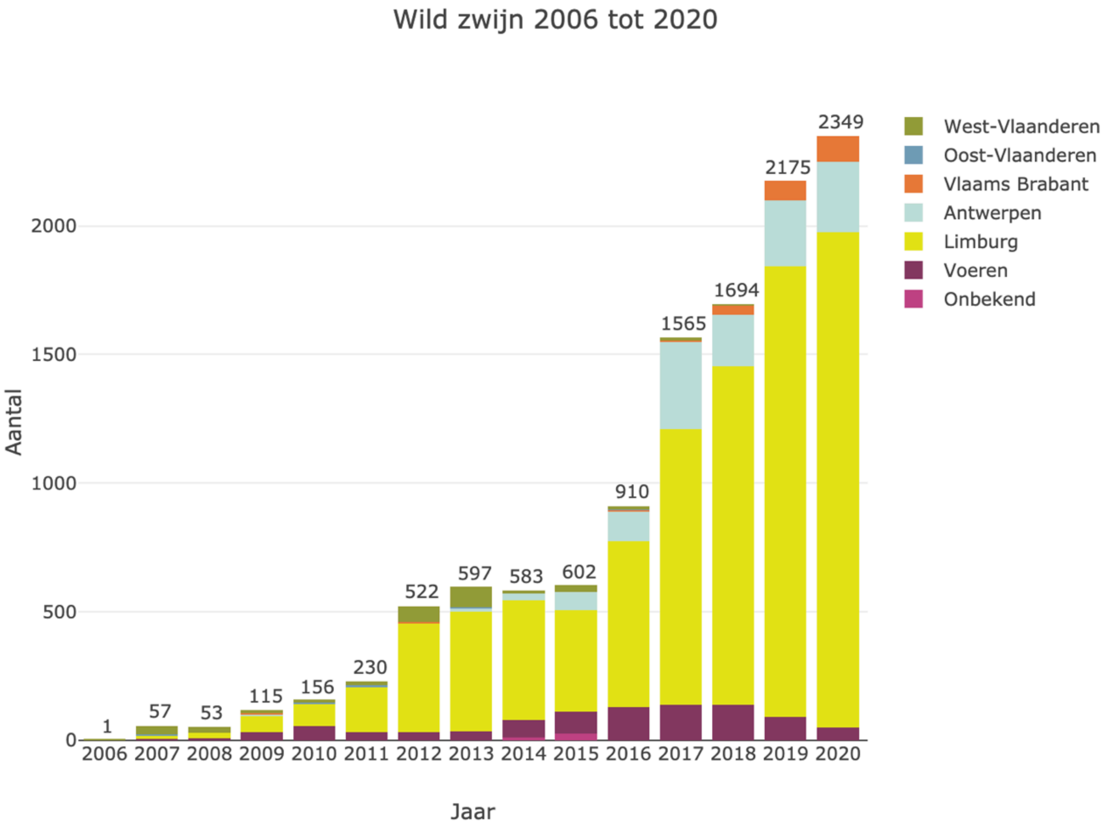


Figure 3: Reported number of shot wild boar per year (2006-2020) in the different provinces of Flanders and for Voeren. Numbers of the bars give the total amount shot in that year (grofwildjacht.inbo.be).

In Flanders, except for the core around Zedelgem, a spontaneous reestablishment occurred from neighboring populations from Wallonia, Germany, and the Netherlands. The population around Zedelgem originated due to active reintroduction and/or negligence (Casaer & Van Den Berge, 2006; Geeraerts et al., 2019). After the establishment of several cores in Limburg, the wild boar distribution further expanded to the northeastern part of the province of Limburg. Later the distribution expanded to the eastern part of the province Antwerp. In Flemish Brabant populations got established in the forest and nature reserves south of Leuven and in the Sonian Forest (Geeraerts et al., 2019; Huysentruyt et al., 2015; Thomas Scheppers & Jim Casaer, 2012). Figure 4 gives the distribution area of wild boar in 2018. This distribution is mainly limited to the eastern of Flanders. However, their distribution is expanding towards the center of Flanders (Rutten et al., 2019b).

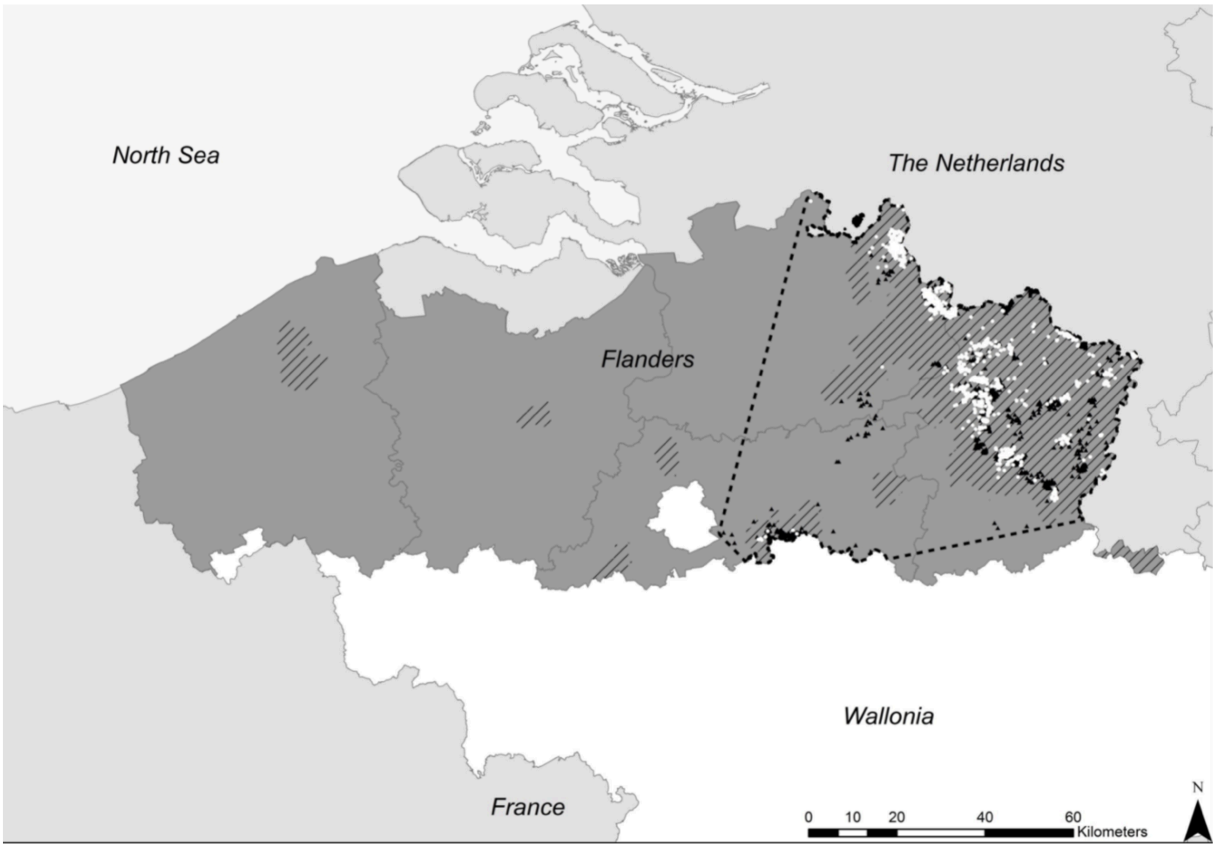


Figure 4: Wild boar distribution in Flanders with occurence records from waarnemingen.be (black triangles, 1383 in total) and locations from hunting bags (white dots, 1510 in total). Dashed areas give known current distribution range of wild boar (based on municipal hunting records). Source: Rutten Citizen science.

In the area of Meerdaal forest, there were irregular sightings in the 1980's and 1990's of vagrant individuals from Walloon populations (Janssens et al., 2004; Vandekerkhove, 2010). From 2006 onwards, more regular sightings of Wild boar were made (Lambrechts et al., 2019). In 2016, the first sightings of new born wild boar were made, and thus proof of local reproduction was recorded (Meuleman & Vanwanseele, 2019). Since then, the population has expanded (for details: see chapter "Materials and Methods 1.1 Wild boar in Meerdaal forest").

2 Characteristics

As you can see on figure 5, wild boars are in general bulky and strongly built. Compared to their bodies they have relatively short and thin legs. Their trunk is relatively short as well, with a strongly developed anterior part and a less developed posterior part. Their back is raised at the level of their shoulder blades and runs into a thick, short neck. Their head is very large and makes up about 1/3 of their total body length. Ears are long and broad. Eyes are rather small and deep-set. They have elongated muzzles with a snout disc and a mouth with large canine teeth of which the lower and upper ones are curved. These canine teeth are more pronounced in males, they have protruding canine teeth which keep growing throughout their life. Their head os well developed for digging and acts as a plow. In combination with their strong neck muscles, they can easily upturn soil. Their ail is thin and short. They have two middle and two lateral well developed hooves, enabling quick movement up to 40km/h. Middle hooves are more elongated and larger than lateral hooves (Geptner et al., 1988; Tack, 2018; Wehr, 2020).

Figure 5: Female wild boar (sow) with sucklings (Tack, 2018)

Sexual dimorphism is notable, in general females are 20-30% lighter and 5-10% smaller than male individuals. Males can also be recognized by a mane running down their back. However; adult weight and size is strongly dependent of habitat, diet and population abundance (Tack, 2018). In general, in Europe there is a west-east and a north-south gradient. Animals living in Eastern Europe are in general larger and heavier than those in Western Europe. Northern opulations -are in general heavier and larger than populations in Southern Europe (Casaer & Van Den Berge, 2006; Goulding et al., 1998). In our region averages for adult males are: 75-100 kg, 150 cm in body length, and 75-80 cm shoulder height. The largest males can weigh up to 200 kg. Averages for adult females are: 60-80 kg, 140 cm body length and 70 cm shoulder height. The largest females weigh up to 120 kg.

They have a brindled bristly coat with a thick, brown underlying fur. The length of these bristles is variable along their bodies. The manes typical for males are formed with these bristles. The color of their coat is variable between region and age. It ranges from light brown or pale yellow to rusty brown and totally black. Piglets have a typical pale brown coat with darker bands (figure 4) (Geptner et al., 1988; Goulding et al., 1998; Tack, 2018).

3 Social groups

Wild boars are social animals living mainly in groups called sounders. These groups vary in size between 6-30 animals (Goulding et al., 1998; Groot Bruinderink & Dekker, 2010). A sounder consists mainly of adult sows and their sucklings. Extended groups also include juveniles of previous litter (Dardaillon, 1988). Sucklings and juveniles in these social groups can be both male and female. Sounders are female dominated, with the healthiest, mostly older, females acting as matriarch. Male offspring leave the sounder when they reach an age of 8-15 months. These subadult males can both live solitary and in small groups. The female offspring often remain with their mothers or establish new groups in new territories. Adult males are mostly solitary, but they do tolerate each other. However, during the breeding season, on average from November to February, they seek for sounders and become more aggressive towards other males (Dardaillon, 1988; Goulding et al., 1998; Groot Bruinderink & Dekker, 2010; Tack, 2018). During this time, these adult males fight each other over females, mate with these sows and continue their search for other female sounders (Leaper et al., 1999). Although subadult males and adult males are living mostly apart, they do occur in overlapping home ranges. Different female sounders also co-exist in the same home ranges, but normally they keep their own social identity (Goulding et al., 1998; Groot Bruinderink & Dekker, 2010). In general, there is a high degree of relatedness in sounders due to female philopatry and the aggregation of related animals. This can facilitate social interactions and social cohesion (Poteaux et al., 2009).

These group structures are dynamic and can change regularly in relation to breeding and farrowing season. For example, during gestation (mainly in April) sows become isolated for a short period prior to giving birth. Later, these newly formed family groups often re-join their sounder or form a new sounder. Also, entry of nulliparous females in existing sounders can occur in autumn (Dardaillon, 1988). The temporarily arrival of adult males in the rutting season leads to the departure of subadult males in their second year of life (Casaer & Van Den Berge, 2006; Leaper et al., 1999). Social groups may also become more fluid and unexpected seasonal assemblages can occur to avoid hunting and predation risk. For example, it is recorded that groups tend to aggregate in times of hunting (Iacolina et al., 2009; Maselli et al., 2014; Poteaux et al., 2009; Wehr, 2020). So, group memberships can change regularly due to fission and fusion of groups and dispersal of individuals when groups become too small are too big (Goulding et al., 1998; Groot Bruinderink & Dekker, 2010; Mayer & Brisbin, 2009; Poteaux et al., 2009). It was assumed that most sounder members were closely related with each other. However, also non-kin associations occur in wild boar social groups, mainly due to the consequences of high hunting pressure. Sometimes even orphaned sucklings get accepted and raised by other sows (Groot Bruinderink & Dekker, 2010; Iacolina et al., 2009)

4 Reproduction and mortality

Wild boar has a true seasonal reproductive lifecycle (figure 5) (Peltoniemi et al., 2000). In relation to body mass, they have the highest potential reproduction rate of all ungulate species. Population reproduction rates can exceed 200% (Keuling et al., 2013). The magnitude of these rates is linked with food availability and weather conditions. Favorable temperature conditions have a positive effect on offspring survival (Geisser & Reyer, 2005; Tack, 2018; Taylor et al., 1998). High food availability has a positive effect on reproduction; females reach their reproductive age quicker, the average litter size increases, and the proportion of breeding females increases as well. Also mast years have a regulatory influence on reproductive rates. The presence of high volumes of energetic mast can lead to a high reproductive output, while the absence of high volumes of mast can lead to a crash in populations and high piglet mortality (Massei et al., 1996).

The rutting season has an interannual variable character, ranging in general from November to February (Groot Bruinderink & Dekker, 2010). However, rutting seasons starting in September and ranging up until March also occur. The interaction of environmental factors like photoperiod, summer rainfall, vegetation development, the occurrence of mast years, housing; and ambient temperature determines this annual variable character (Ahmad et al., 1995; Baber & Coblentz, 1987; Mauget, 1982; Peltoniemi et al., 2000). As said above, during this period males actively search for sounders, fighting aggressively with each other to show their dominance. The most dominant males, often the largest, mate most frequently. Sows must reach a critical weight threshold of 25-30kg to be able to participate in the reproduction. On average, females reach this threshold from the age of 2. However, when conditions are favorable, and food is readily available they can be sexually mature after only 7 months (Groot Bruinderink & Dekker, 2010; Mauget & Pépin, 1987; Tack, 2018). The proportion of reproductive females varies between 90-11% based on food availability (Leaper et al., 1999). Males only participate in reproduction after 4-5 years. In recent years in Europe, the female reproductive age has lowered in general (Groot Bruinderink & Dekker, 2010). This increase in reproductive success is contributing to the observed population and range expansion in Europe and Flanders.

The gestation period ranges between 114-130 days for first time breeding females and between 113-140 days for older sows. Giving birth or farrowing occurs mostly in spring between March and May, with a peak in April. Sows give birth in a farrowing nest, which is built using standing vegetation from the direct proximity of the nest. Average nest size lays between 4-6 piglets, but this can range between 1-12 depending on the health and age of the sow (Groot Bruinderink & Dekker, 2010; Heptner et al., 1988; Tack, 2018). The mother and its offspring stay for 4-6 in the farrowing nest, later they rejoin the group or form a new sounder. The piglets keep suckling up to 3.5 months. However, they do start with adult feeding behavior after only 2-3 weeks. They are fully weaned after 4 months (Tack, 2018). After 4-6 months the body weight of the young can reach up to 20kg, after 13-15 months this has doubled to 40kg. In normal conditions female wild boar are infertile in summer. But, in favorable years a late or second nest is possible during summer or in autumn (Groot Bruinderink & Dekker, 2010; Tack, 2018).

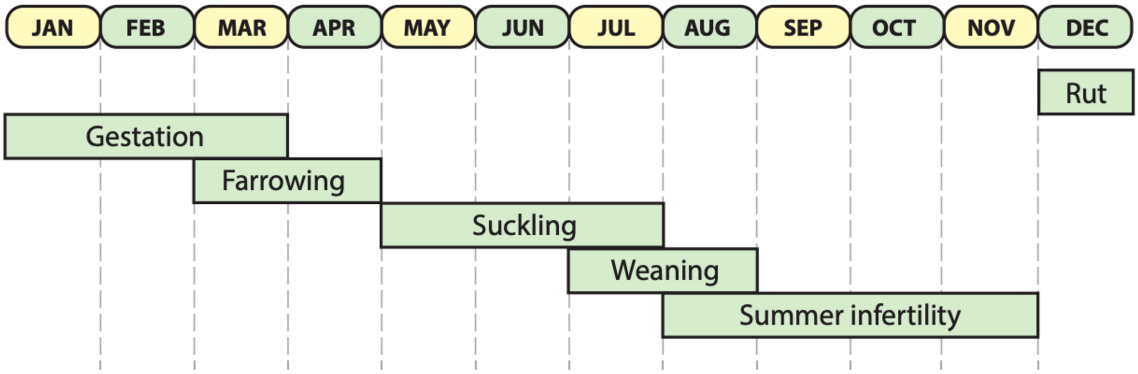


Figure 6: General reproductive lifecycle of an adult wild boar sow (Tack, 2018)

The max lifespan of wild boar is 10-14 years, but only few individuals survive past the age of 4-5 years (Tack, 2018). Main causes of natural mortality are predation, starvation due to bad weather and food conditions and diseases. In Flanders, and most other parts of Europe, predation is negligible (Groot Bruinderink & Dekker, 2010; Okarma, 1995). Other important causes of death are car accidents and hunting. Hunting is by far the most important reason of mortality. Almost all populations in Europe are regulated by hunting (Groot Bruinderink & Dekker, 2010; Massei et al., 2014; Tack, 2018). But, for European populations the relative mortality caused by hunting has decreased over the last few decades. Which can indicate that recreational hunting alone may currently not be sufficient to limit population growth. Therefore, professional hunting and hunting for the protection of agricultural activities may become more important in the future than sporting/recreational hunting to control wild boar populations (Massei et al., 2014).

5 Diet

Identifying the diet of species can help in understanding how they use different ecosystems and therefore determining its role in the food web (Baubet et al., 2004). For this, diet composition studies are crucial. By doing so we might be able to predict when and why some plant and or animal communities might be damaged (Wood & Roark, 1980). The diet of wild boar has been studied frequently and quite well, both in its native range as in introduced areas. Four main feeding behaviors can be distinguished: browsing and grazing of grasses, leaves, stems and herbs; foraging on the ground for fruits, animal matter and fungi; predation of both vertebrates and invertebrates; and rooting for rhizomes, roots, bulbs, tubes and other belowground food sources (Ballari & Barrios-García, 2014). In general, above ground parts of plants are more important than below ground parts, although variation in importance occurs (Ballari & Barrios-García, 2014; Leaper et al., 1999)

Wild boar are omnivores with a highly flexible diet. They are monogastric, making them less able than ruminant ungulates at digesting cellulose and green plant matter. Therefore, often energy rich food is needed in their diet (Leaper et al., 1999). Heptner (1988) divides the diet into four groups: rhizomes, roots, tubes and bulbs; fruits and seeds, also called mast (Schley & Roper, 2003); above ground plant parts; and items of animal origin. Schley & Roper (2003) add agricultural crops as an extra important group. The diet consists primarily of plant matter, generally speaking 90% of the total uptake is made out of plants. The other 10% consists mainly of animal matter. According to a review done by Barrios-Garcia & Ballari (2012), the volume of plant matter tends to be slightly greater in the native range of wild boar (>90%), than in its introduced range (87%). The volume of animal matter ranges in native areas between 1-16% and in introduced area between 2-33%. Although being low in volume, they do eat animal matter frequently. It seems to be an essential dietary compound for essential proteins. Its high due digestibility makes it an important food source as well (Casaer & Van Den Berge, 2006; Fournier-Chambrillon et al., 2014). Animal matter includes mammals, birds, reptiles, amphibians, invertebrates like insects, snails and earthworms and crustaceans. Of which insects, earthworms, mammals, and birds are the most consistently found in the diet of wild boar. Animal matter can be both prey or carrion (Schley & Roper, 2003). Sometimes, if easily available, they also eat relative high amounts of fish. For example in areas or times where dry river beds occur (Dardaillon, 1987; Heptner et al., 1988). This illustrates that in general rarely eaten foods can be eaten in high volumes if they are easy and readily available (Schley & Roper, 2003). More uncommon food items like algae, human waste and inorganic material such as stones and plastic, the latter may be accidently, are also found in their diet (Ballari & Barrios-García, 2014; Hafeez et al., 2011). A compiled list of all species found in the diet of wild boar in Europe is given by Schley & Roper (2003). For the construction of this list they used information from 21 dietary studies carried out in Europe.

Remarkably, most studies do not document consumption of fungi, although widely present in Europe’s forests. In two studies the occurrence of fungi in wild boar’s diet is 46% and 60% (Abáigar, 1993; Fournier-Chambrillon et al., 2014). Fungi are probably also a regular part of the diet, but due to the high digestibility it is unlikely to be detected in feces samples and can only be found in stomach samples when eaten very recently (Schley & Roper, 2003).

Although the diet being very broad, there still is a tendency to concentrate on some favored highly digestible and nutritious food items. Especially if they are abundant, like mast (acorns, beechnuts and sweet chestnut) and grain plants (Goulding et al., 1998; Herrero et al., 2005; Schley & Roper, 2003). There is always at least one such energy rich plant food found in their diet. Agricultural crops are also an important part of the diet in Western Europe (Fournier-

Chambrillon et al., 2014; Schley & Roper, 2003). The food selection can vary depending on the presence of different crops or by positive selection of some crops over other. In general, maize is one of the most preferred agricultural products (Ballari & Barrios-García, 2014; Casaer & Van Den Berge, 2006; Schley & Roper, 2003). Sometimes populations are even heavily dependent of agricultural products, in those cases crops can be up to 90% of the total diet (Herrero et al., 2006). Products like maize are also often given as supplementary feeding by hunters, making the interpretation of their natural diet harder (Casaer & Van Den Berge, 2006). Although it is suggested that in cases where natural foods, such as mast, are in abundance wild boar will not use or need additional foods like agricultural crops (Sjarmidi et al., 1991).

So, in general fruits and seeds or mast are the most important part of the natural diet. Hence, wild boar can often act as seed dispersers or seed predators (Ballari & Barrios-García, 2014; Casaer & Van Den Berge, 2006). But as said above, food selection is very variable. It depends on food availability, temporal variations, geographical variations, and energy requirements, like for example between different age classes (Ballari & Barrios-García, 2014; Groot Bruinderink et al., 1994; Schley & Roper, 2003).

Temporal variations can be divided in seasonal and interannual variation. Seasonal variation is mostly explained by food availability. Logically, rooting for below ground matter is more important in winter while above ground green matter is more important in spring (Baubet et al., 2004; Scott, 1973). Interannual variation is mostly due to the presence of mast years, in these years the consumption of mast starts in autumn and can continue until spring. In these mast years other plant matter is consumed less, both in volume and in frequency. Indicating again that mast is the favored diet. Yet, there seems to be no difference in the consumption of animal matter. In mast and in non-mast years the consumption of animal food stays important. It is found that the presence of mast years either increases are fails to affect the consumption of animal matter (Groot Bruinderink et al., 1994; Schley & Roper, 2003). This indicates that animal and plant foods are not substitutable, a small percentage of animal matter seems important for the survival and growth of wild boar. There is also a noticeable amount of geographical variability, again reflecting food availability (Schley & Roper, 2003). For example, in coniferous forests the diet is based on a mix of tree bark, underground food, invertebrates and carrion (Leaper et al., 1999). And again according to its availability, in some areas grasses are more important while in other areas leaves form an important part of the diet (Casaer & Van Den Berge, 2006; Chimera et al., 1995).

Especially rooting for below ground food sources can cause ecosystem level effects (Barrios-Garcia & Ballari, 2012; Massei & Genov, 2004). It is logical that there is a positive correlation between rooting intensity and the consumption of underground food sources. Rooting is done mostly for the consumption roots and bulbs (Baron, 1982; Genov, 1981; Scott & Pelton, 1975). Therefore, this can be seen as the most important feeding behavior for this study. The importance of underground food sources and rooting in the diet of wild boar is however also variable. Some studies attribute a high importance to below ground parts (Baubet et al., 2004;

Challies, 1975; Eriksson & Petrov, 1995; Scott & Pelton, 1975), while authors argue that roots and bulbs or of little or no importance (Fournier-Chambrillon et al., 1995; Genov, 1981; Herrero et al., 2005; Irizar et al., 2004; Massei et al., 1996; Wood & Roark, 1980). For example, a study in the French Alps found that roots and bulbs represented up to 39% of the average annual diet. In winter this even peaked to 61%, indicating a strong seasonal effect. Also, a strong effect of elevation was found. The relative use of roots and bulbs increased from 16% for populations below 1500m to 71% for areas above 1900m (Baubet et al., 2004). Similar results were found in other dietary studies in mountainous areas carried out in the Smoky mountains (Scott & Pelton, 1975) and on the Auckland Island (Challies, 1975). In Mediterranean habitats, below ground food items are of less importance. There it is found that the diet is mainly based on fruits (Fournier-Chambrillon et al., 1995; Massei et al., 1996; Wood & Roark, 1980). In habitats including agricultural land, food habits depend strongly on cultivated crops. Not only roots and bulbs, but also earthworm consumption is an important part of their belowground diet (Baubet et al., 2004; Challies, 1975; Howe et al., 1981; Scott & Pelton, 1975; Wood & Roark, 1980). Although being of less significance in terms of rooting disturbance because animal matter is only a marginal part of their diet (± 10%). This indicates that the importance of below ground feeding, and thus of rooting, is variable due to geographical and seasonal variety as well. In general, rooting intensity increases with increasing food scarcity. Wild boar also repeatedly re-root the same areas within their home range (Bruinderink & Hazebroek, 1996; Falinski, 1986; Goulding, 2003; Sims, 2006). Therefore, according to Sims (2006) they can be considered as a major disturbance for these frequently visited areas.

6 Habitat and home range

6.1 Habitat

Its broad diet makes wild boar a eurytopic species. This opportunistic omnivore has a very wide range of habitats ranging from temperate forests to grasslands, taigas, tropical forests, mountains, and semi-arid environments (Goulding et al., 1998; Heptner et al., 1988; Massei et al., 2011; Tack, 2018). They can even be found in coastal swamps, riparian environments and brackish and fresh marshlands (Goulding et al., 1998). Also, they are well able to live in anthropogenically altered environments. The species can also adapt to habitats with altering agricultural patterns. In these habitats they often largely rely on agricultural crops or even human garbage (Hafeez et al., 2011; Schley & Roper, 2003; Wehr, 2020).

The preferred habitat in Europe are deciduous and mixed forests that are enclosing marshes and meadows. Less preferred are coniferous forests and heathlands (Geptner et al., 1988; Goulding et al., 1998). Some elements are especially important in order to survive in a given habitat: food availability, shelter, weather conditions and the presence of water (Leaper et al., 1999). Since they prefer high energetic food sources, suitable habitats should produce abundant and diverse food sources. Especially fruit bearing deciduous trees such as beech, oak, hazel, and sweet chestnut have an important function. The presence of secure areas for protection against predators and bad weather conditions are also important habitat requirements. For this, they construct resting places and hideouts. In natural habitats, these hideouts and shelters often consist of thick brush or are made of grasses, spruce branches litter and other vegetation gathered in the proximity of these nests. In anthropogenic landscapes often agricultural fields are used as resting places. These places are often close to streams, in shrub thickets or in tall grass. They tend to avoid extreme weather conditions such as regular snowfall or long periods of droughts. The presence of water is not only desired for drinking, but since sweat glands are lacking water is also essential for wallowing to cool down in warm summer periods (Goulding et al., 1998; Heptner et al., 1988; Keuling et al., 2008a; Leaper et al., 1999; Mayer et al., 2002; Tack, 2018). Spatial segregation between sexes occurs, subadult males mainly prefer habitats for its food potential. On the other hand, females with piglets rather pick habitats which provides a combination of security and food potential (Spitz & Janeau, 1995).

6.2 Home range

Groups of wild boar or individual wild boar are usually more or less confined to permanent sites or home ranges. These home ranges can change seasonally and interannual. Often home ranges are largest in autumn, especially when food is scarce (Heptner et al., 1988; Iacolina et al., 2009). The size depends on several factors. Some important ones are the distribution and availability of food, the presence of water, shelter opportunities, general habitat quality, age, sex, density of the population, social group size, predation and hunting, weather conditions and habitat disturbances (Casaer & Van Den Berge, 2006; Goulding et al., 1998; Leaper et al., 1999). Therefore, the size can vary considerably across different regions or areas. Females have in general smaller home ranges than adult males (Casaer & Van Den Berge, 2006; Leaper et al., 1999). A large variety of home range sizes can be found in literature. According to Moore & Wilson (2005) home range sizes of females living in sounders varies between 1.4 and 54.1 km^2. While home range size of males varies between 2.8 and 25.7 km^2. Sometimes home ranges of more than 154 km^2 are found. Spitz & Janau (1990) suggest on a review of several European studies that mean home ranges are small ($4km^2$). Normally different female sounders do not defend their home ranges, so overlapping of home ranges is common. This facilitates mixing of individuals and gene flow (Moore & Wilson, 2005; Wehr, 2020). On the other hand, the home ranges of males are more exclusive (Boitani et al., 1994).

Home ranges can be divided in areas feeding and core areas. These core areas are important for providing security and preferred nesting areas. As said, home ranges of females overlap commonly, the core areas however tend to show no overlap (Goulding et al., 1998). The core areas of males are in general larger and more fragmented and dispersed throughout their home ranges (Boitani et al., 1994; Goulding et al., 1998). Females show a large fidelity towards these core areas and spend more time here than males (Casaer & Van Den Berge, 2006; Iacolina et al., 2009; Keuling et al., 2008b). Splitting of feeding area and core area for resting can be an anti-predation strategy (Spitz & Janeau, 1990).

Human disturbance, and particularly hunting, can have effects on the home range magnitude. Both an increase in home range size due to hunting (Calenge et al., 2002; Sodeikat & Pohlmeyer, 2002), as a decrease in size (Keuling et al., 2008b; McIlroy & Saillard, 1989) has been recorded. This effect may depend on the amount of human disturbance these populations have experienced in the past. A constant and high hunting pressure for example can cause boars to hide and lie still instead of expanding their home range in times of hunting (Dexter, 1996). According to Keuling et al. (2008b) there seems to be two major anti-predator strategies: 1) shifting or enlarging home ranges to escape hunters, and 2) staying in the known home range and even reducing space into more secure places within this home range.

Impacts

The recent increase in both abundance and distribution of ungulate species, including wild boar, in Europe and Flanders leads to an increase in conflicts between humans and these animals (Tack, 2018). For wild boar, this increase is partly caused due to their wide range of possible habitats and their plastic diet. Also, their high reproductive rate and the changing socio-economic factors play a role in this increase. Because of this increase, wild boar can have a substantial social, economic and environmental impact (Ballari et al., 2015; Massei & Genov, 2004). The impacts they have are subjective. These are always seen from a human point of view, based on what is regarded as desirable or undesirable for us humans. It also depends on where you are and on what the management aims, or economic goals are. Disturbance in industrial timber forests can be of greater economic importance than the same disturbance in a nature reserve. Also hunting on and hunting traditions of wild boar determines the attitude towards them. Hunting can provide economic benefits, balancing damage caused by wild boar. For example, in many European countries like Germany, France and Poland damages to forests and agriculture is compensated by the government with earnings gained through hunting (Casaer & Van Den Berge, 2006). According to Young et al. (2010) the presence of wild boar can lead to two major groups of impacts or interactions; interactions between humans and the animals, called human-wildlife impacts (Young et al., 2010), and possible conflicts between people about the needed wildlife management, called human-wildlife conflicts (Geeraerts et al., 2019; Young et al., 2010). Especially the human-wildlife impacts will be discussed further.

1 Socio-economic impacts

There are many socio-economic impacts of wild boar, these can be both negative and positive. Examples of negative impacts are: risk of agricultural damage, possibility of spreading disease to livestock, possibility of spreading disease to humans (zoonoses), traffic accidents, possibility of unsafe encounters, damage to private property and gardens, damage to public properties and garbage raiding in cities (Cahill et al., 2012; Geeraerts et al., 2019). Positive effects are: the opportunity to hunt on wild boar, opportunity of sightings of these animals, availability of sustainably harvested meat and the extra earnings out of tourism and recreation due to the presence of wild boar (Geeraerts et al., 2019). The earnings from renting of hunting grounds can increase strongly when wild boar is included in the hunting bag, creating an important positive economic impact.

Especially the impacts on agriculture have been of great interest and have been studied well (Barrios-Garcia & Ballari, 2012). Each year tens of millions of euros are paid by EU governments and hunting right owners to compensate for damages and losses of income (Calenge et al., 2004; Frackowiak et al., 2013; Mazzoni della Stella et al., 2014; Schlageter & Haag-Wackernagel, 2012; Tack, 2018; Vassant, 1997). Energy rich agricultural crops can form a great part of their diet. Most of the time the crops are either affected at the end of their growing period when they bear ripe fruit or just after sowing when seeds and seedlings are rooted out of the soil (Casaer & Van Den Berge, 2006). The distance between resting places and agricultural fields plays an important factor in the risk of damage. When resting areas are in a forest core, more than 2km from the forest edge, foraging is mostly concentrated in the forest. When resting areas are less than 1km from agricultural fields, lots of damage can be expected (Hahn & Eisfeld, 1998). Also the density of wild boar and the availability of natural fruits/food plays on important role (Massei & Genov, 2004). Not only direct feeding causes damages, also trampling of crops, rooting, laying, and rolling causes important indirect damages. Also, pastures can get damaged, often large parts of these grasslands get turned over by wild boar searching for fungi, bulbs, roots and invertebrates like worms and larvae (Alexiou, 1983; Casaer & Van Den Berge, 2006; Cocca et al., 2007). Direct damage to livestock rarely occurs, although sometimes problematic killing of young animals like lambs has been documented. These incidents mainly occur in introduced populations like in Australia (Choquenot et al., 1996).

Wild boars can also be important vectors for diseases. These diseases can be transmitted to domestic pigs and other livestock. It is logic that higher risks occur when there is overlap between pastures and the home ranges of the wild boar. Wild boars often have high population densities and high mobility, increasing the chance and speed of spreading of diseases (Casaer & Van Den Berge, 2006; Groot Bruinderink & Dekker, 2010).

Another important socio-economic impact is traffic accidents. Together with the increase of ungulate species in recent decades, the amount of traffic accidents also increases (figure 6). A study at the Veluwe (Netherlands) clearly shows this increase in traffic accidents caused by wild boar (Bruinderink et al., 2010). They found two yearly peaks in the number of accidents. The first one appears in May/June when piglets born in April/May start to undertake tours with their mothers. A second peak is observed in October/November, prior and during the reproductive period. Piglets until the age of 12 months cause the most. Other factors increasing the chance of traffic accidents are local population densities, habitat fragmentation, the location of roads through their habitat and roads between resting and foraging areas (Casaer & Van Den Berge, 2006). Preventive measures like fencing of highways passing through habitats of wild boar, together with ecoducts to prevent isolation, can reduce the chance of accidents (Bruinderink et al., 2010; Groot Bruinderink & Dekker, 2010).

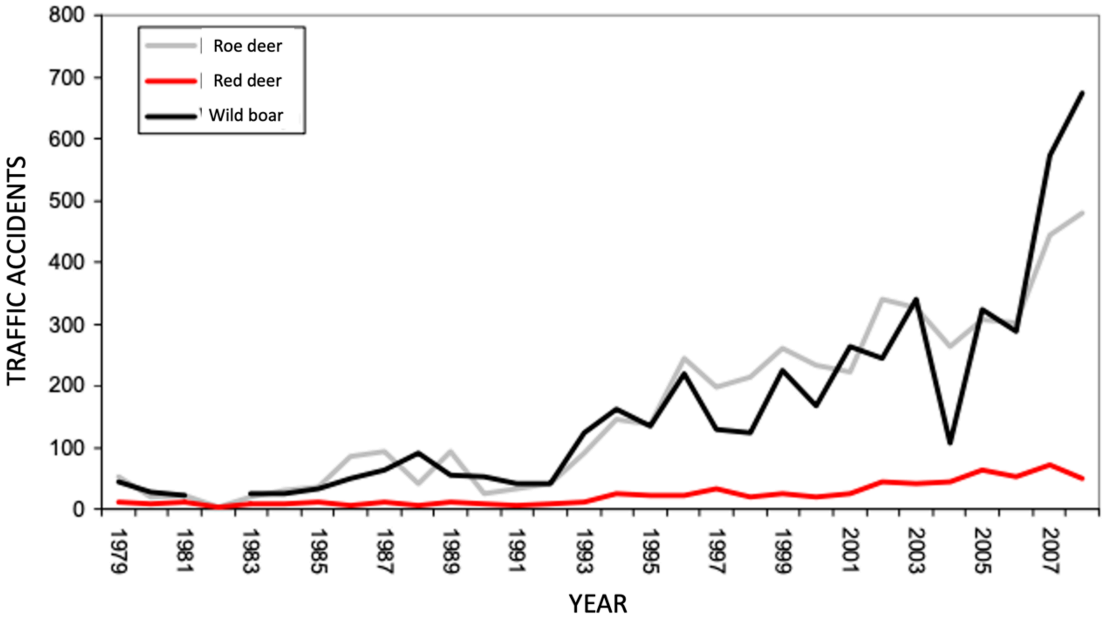


Figure 7: Number of traffic accidents for three ungulate species at the Veluwe in recent decades. Adapted from Bruinderink et al. (2010).

2 Environmental impacts

Wild boars are called ecosystem engineers. They can vastly influence species abundance, species richness, food webs, ecosystem dynamics and soil chemistry. They affect species through direct herbivory and predation, through changing the availability of resources available to other organisms, through modifying, creating or maintaining their habitats and through altering soil structure and texture, causing for example erosion (Ballari et al., 2015; Groot Bruinderink & Dekker, 2010; Massei & Genov, 2004; Mauri et al., 2019). Especially their rooting behavior can create ecosystem level effects (Barrios-Garcia & Ballari, 2012; Massei & Genov, 2004; Tack, 2018). Welander (2000b) describes rooting as a recurrent disturbance regime, varying in extent and frequency.

Ecological disturbances in general can be seen as a biological or non-biological event that kills organisms and brings alteration in their spatial patterning in the habitats or ecosystems they inhabit (Paine, 2019). Disturbances play a significant role on all ecological levels, ranging from the individual level to the biosphere. Disturbances can be of different magnitude, both in intensity, duration, and frequency. An important and well-known hypothesis examining the effects of disturbance on species diversity is the “intermediate disturbance hypothesis”. This hypothesis, originally presented by Connell (1978), states that intermediate frequency and intensity of disturbance will maximize species diversity. At low disturbance regimes, species diversity will be low due to the domination of some competitive species. At high disturbance frequency/intensity, species diversity will be low due to too much biodiversity loss. In the light of this hypothesis, wild boar rooting can have both negative and positive effects according to the magnitude of disturbance.

As said before, wild boar tend to re-root the same areas within their home range (Bruinderink & Hazebroek, 1996; Falinski, 1986; Goulding, 2003; Sims, 2006). Therefore, rooting intensity within their home range is variable. Some areas will undergo high rooting pressures since they are more suitable for wild boar, while others will undergo none or low rooting pressure. Wild boar activity can enhance structural and spatial heterogeneity by small scale disturbances. With their rooting behavior wild boar constantly create patches of various kinds, resulting in a mosaic of spatially and temporally variable biophysical patches. This increases structural complexity of the habitat and the soil. This enhanced spatial and structural heterogeneity affects species diversity, composition and ecosystem functioning (Welander, 2000b). The study of Welander (2000b) shows that rooting causes a relatively foreseeable disturbance regime between habitat types and soil category. Nevertheless, this disturbance regime varies in size interannually (Bruinderink & Hazebroek, 1996; Welander, 2000b).

The environmental effects of wild boar are controversial, assessing impacts on aspects like species composition, richness and dynamics is not straightforward (Barrios-Garcia & Ballari, 2012; Leaper et al., 1999; Tack, 2018). There are many known impacts, these can be both positive, negative, neutral, and varying between studies and habitats. For example, it is found that rooting intensity is higher in deciduous forests than in coniferous forest (Bruinderink & Hazebroek, 1996; Fonseca, 2008; Welander, 2000b). The environmental impact is logically dependent on the disturbance regime. In accordance with the intermediate disturbance hypothesis it is predicted that the highest species diversity can be expected at intermediate levels of disturbance (Connell, 1978). This means that with moderate wild boar densities, leading to moderate disturbance regimes, the environmental impact is likely to be mild or even beneficial (DEFRA, 2008a; Wilson, 2005). At higher densities, leading to larger disturbance regimes, impacts on the same attribute can be negative (Welander, 2000b).

Impacts also depend on local habitat, habitat history and species. Some species are better adapted to disturbance and can get favored due of this rooting behavior. Wild boars were and still are part of the natural ecosystem in Europe and Flanders. Therefore, these natural ecosystems are adapted to its presence. In areas where it is introduced, it can be disrupting non adapted ecosystems. This can lead to the extermination of vulnerable species. Yet still, due to unnatural overpopulation and the absence of wild boar for decades in Flanders and other parts of Europe, they are likely to exert an impact on some (semi-) natural habitats that now are of conservation value (Casaer & Van Den Berge, 2006; DEFRA, 2008a).

As said, rooting is the most important behavior in terms of impacts. However, also other types of feeding behavior, rubbing trees, wallowing, and building nest can exert impacts. Fungal species can probably form a significant part of wild boar's diet. Therefore, effects on fungal communities can be important but these are largely unexplored. Only very little is known about overall effects on fungi populations (Barrios-Garcia & Ballari, 2012). Piattoni et al. (2014) studied the effect of the passage of *Tuber aestivum* asci and ascospores through the gastrointestinal tract of wild boar. They found that the passage through the guts freed the spores, modified the structure of these spores, and eroded the spore walls. It is believed that these modifications might be linked with the observed increase in the formation of mycorrhizas with oak trees. This supports the theory that wild boar can play a significant function in truffle range expansion and survival during climate change (Büntgen et al., 2012; Hall & Zambonelli, 2012; Piattoni et al., 2012; Splivallo et al., 2012; Trappe & Claridge, 2005).

In Argentina, where wild boar has been introduced in the 1900s, the effects of wild boar and other native and non-native mammals on the abundance and diversity of fungal spores have been studied several times (Aguirre et al., 2021; Nuñez et al., 2013; Soteras et al., 2017). For these studies fecal samples of wild boar were collected and examined with molecular, observational and greenhouse experiments. Soteras (2017) found that both native and non-native fungal spores were present in almost all tested fecal samples. Other research found that wild boar and deer seemed to be the most important vectors for ectomycorrhizal fungi dispersal linked with Pinaceae species (Aguirre et al., 2021; Nuñez et al., 2013). Which is not surprising since it is known that they act as spore dispersers in their native ranges (Ashkannejhad & Horton, 2006; Génard et al., 1988). Mycophagous animals can concentrate vast amounts of fungal spores in their feces and move these spores over different habitats and distances (Aguirre et al., 2021). Similar results were found in a greenhouse bioassay study in Israel, wild boar feces increased the abundance of ectomycorrhizal fungi communities linked with the occurrence of *Pinus halepensis* (Livne-Luzon et al., 2017). This evidence of the importance of wild boar for long distance dispersal of ectomycorrhizal fungi indicates that they might alter the local occurrence, distribution and composition of fungal communities and their obligate symbiotic partners like pine trees (Aguirre et al., 2021; Livne-Luzon et al., 2017; Nuñez et al., 2013; Soteras et al., 2017). The combination of their wide home ranges and their opportunistic diet, counting many hypogenous and epigenous fungi (Génard et al., 1988; Piattoni et al., 2012), makes wild boar excellent seed and spore dispersers (Livne-Luzon et al., 2017). Especially in regions where forests are strongly fragmented and surrounded by a poor ectomycorrhizal hostplant matrix (Livne-Luzon et al., 2017).

2.1 Impacts on flora

The combination of their omnivorous diet and their typical rooting behavior causes that wild boars play an important role in the dynamics of forest and other ecosystems. They are probably the most important natural modifiers of plant communities (Gilliam, 2007; West et al., 2009). Massei and Genov (2004) made a review study which summarizes the environmental effects of wild boar on both plants and animals (figure 8 and 9).

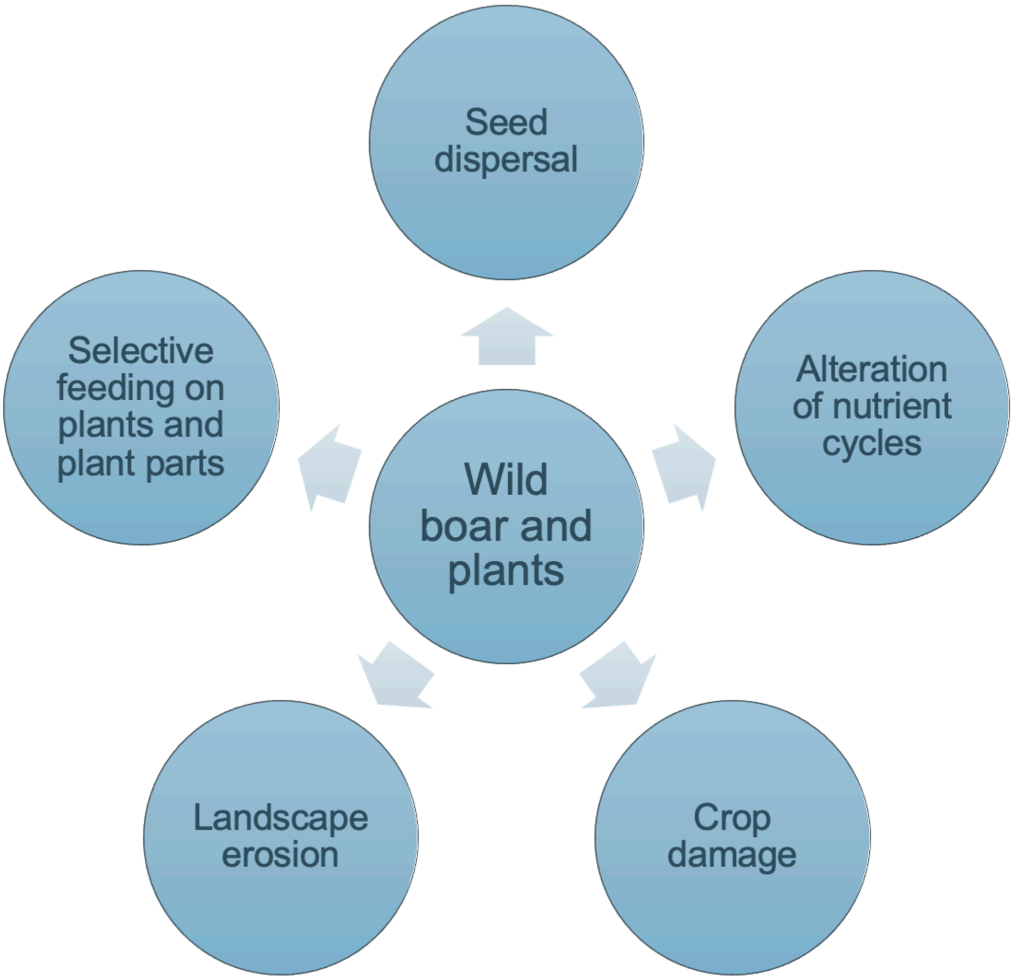


Figure 8: Impacts of wild boar on flora. Adapted from Massei and Genov (2004)

Positive effects of wild boar are accelerating the nutrient cycle and the decomposition of organic material, increased mineralization rates, reduced forest litter depths and amount of leafy material, increased forest growth, clearing of large patches of grass vegetation, promoting natural regeneration of some plant species, removal of competitive plant species via their diet and rooting behavior in the benefit of more rare species and increasing species richness in some cases (Casaer & Van Den Berge, 2006; Singer et al., 1984; Welander, 1995). Welander (1995) concluded in his study that the reintroduction of wild boar in Sweden led to an increase in plant biodiversity. The wild boar recreates a former common disturbance regime. They were native in the past and therefore lots of plants got adapted to the past disturbances caused by wild boar. The return of wild boar led to the restoration of this former disturbance regime.

Also plant communities in areas where other frequent natural disturbances occur can be preadapted to disturbances by wild boar. This can even lead to more resilient plant communities (Baron, 1982; Kotanen, 1995). A study in California, where wild boar are exotic species, found that in the first year the species richness decreases. This decrease got followed by an increase in later years due to wild boar disturbance (Kotanen, 1995). It can also lead to changes in species composition, plants like common bracken (*Pteridium aquilinum*) and several *Poa spp.* recover easily from rooting and can get favored in this way (Groot Bruinderink & Dekker, 2010). Putman (1986) found that grazing had detrimental effects on species such as hawthorn (*Crateagus sp.*), blackthorn (*Prunus spinosa*) and hazel (*Corylus avellana*). More resistant species, like holly (*Ilex aquifolium*) can show expansion under herbivore pressure. Rooting also creates good seedbeds for plants that need bare soil and light in order to germinate. This can result in higher species richness (Groot Bruinderink & Dekker, 2010). Wild boars can also act as seed dispersers (epi- and endozoochory), although other studies state that they mainly act as seed predators (Barrios-Garcia & Ballari, 2012; Groot Bruinderink & Dekker, 2010).

Positive impacts on species abundance are possible. However most studies agree on a negative impact on plant abundance. The effect on species richness is more controversial (Massei & Genov, 2004). As said, some studies found an increase in species richness (Kotanen, 1995; Welander, 1995), other found a decrease in species richness (Bratton, 1974, 1975). Extensive rooting can lead to a reduction in plant cover, which can be associated with the loss of diversity and changes in composition. There is evidence that suggests that the impacts of boars can be critical in situations involving sensitive and endangered species (Barrios-Garcia & Ballari, 2012; Howe et al., 1981; Leaper et al., 1999). If density of boar is high, reductions up to 80-95% of herb cover can occur. Reducing density of seedlings by 1.5-5 times. This can lead to local extinctions of some plant species (Massei & Genov, 2004). Another negative effect is the decrease in natural regeneration of some tree species with increasing rooting intensity and the consumption of mast and seedlings. For example, the reduced regeneration of beech (*Fagus sylvatica*) and oak (*Quercus sp.*) trees found at the Veluwe (Bruinderink & Hazebroek, 1996; West et al., 2009). No effect was found between rooting intensity and the regeneration of other tree species like birch (*Betula sp.*), American black cherry (*Prunus serotina*), holly (*Ilex aquifolium*) and rowan (*Sorbus aucuparia*). Indicating that the net effects on woodlands may differ between habitats and locations and is dependent on rooting frequency. Rooting can also facilitate the establishment of exotic species, alter bacterial communities, cause problems in aquatic ecosystems and can cause erosion (Ballari et al., 2015; Bratton, 1974; Kaller et al., 2007; Oldfield & Evans, 2016; Tierney & Cushman, 2006; West et al., 2009). Invasive plant species often favor disturbed areas and are in general quick colonizers (West et al., 2009). However, it is not sure that rooting is the cause for the observed increase in invasive alien species, or that wild boar are drawn towards areas with higher abundances of exotic species (Barrios-Garcia & Ballari, 2012). Consequences of wild boar and rooting behavior on plant fitness are barely studied.

2.1.1 Impacts of ungulates on plant communities

In all natural or semi-natural system where ungulates occur, they are bound to have a significant influence upon the plant communities. Altering perhaps diversity, productivity and vegetational structure (Frerker et al., 2013; Putman, 1986). Typically, herbivores remove only something in the region of 10% of the yearly green-matter production of a plant community. But in certain instances, for example due to unnatural overpopulation, their impact may be far larger than this (Putman, 1986). Patterns of habitat use are complex. Therefore, animal pressure is by no means distributed evenly over the habitat. Certain vegetation types are perhaps favored for shelter. Some are rarely used, and thus no subject to trampling. Others are preferred for feeding, and thus subject to herbivory, trampling and rooting activity (Coughenour, 1991; Putman, 1986; Wallis De Vries, 1996). Therefore, even within one forest system, certain communities receive little herbivore pressure, while favored sites may show high herbivore influence. This leads to a patchy impact on different plant communities.

Many ungulate species, including wild boar, indeed feed very selectively. This means that often they avoid some species and specifically select others. This can lead to changes in relative abundance and composition of the different components of the natural vegetation. Particularly, graze-sensitive species can get eliminated while resistant or tolerant species may gain dominance. This can affect the species diversity and species composition of many plant communities. Under heavy herbivore pressure, even moderately tolerant species may be eradicated. Especially species that are particularly palatable can experience negative impacts (Putman, 1986). Selective feeding can also be more subtle, favoring specific plant parts or plants of younger ages. This can result in changes in physical structure and age structure (Apollonio et al., 2010; Bullock et al., 1995; Putman, 1986).

Note that plant species behave differently to different herbivore pressures and to different herbivores (Putman 1986). Where light herbivory and defoliation is sufficient to depress productivity, continued herbivory can result in the eradication of plant species from the plant community. Hence, herbivory can depress or stimulate the productivity of individual plants. Through the effect on the individual plant, herbivory and rooting can lead to changes in plant community composition. Even light herbivory, for example mild defoliation, may still exert a profound effect on community level. By reducing the biomass of preferred species, the herbivores can reduce competition for space and light. Consequently, less competitive plant species may be able to colonize and increase in abundance in communities where they would normally be outcompeted (Huntly, 1991; Putman, 1986; Vázquez, 2002). Moderate or high levels of grazing can therefore significantly change entire species compositions. A frequently noted response to heavy grazing is a shift in community structure to more grass species. Grasses grow from the base, making them less sensitive to grazing (Putman, 1986; Rooney & Waller, 2003). Other well adapted species to grazing and trampling are low growing species, clonal species and rosette plants.

The actual result will depend on the specific herbivore, the degree of herbivory, the timing at which damage occurs, the possible preadaptation of vegetation to herbivory, and the particular plant species in the community (Putman, 1986). Herbivores not only affect species composition of the vegetal communities directly. Also, indirect effects, such as the impact on the nutrient cycling, may have further repercussions for the community composition and productivity (Crawley, 1983; Massei & Genov, 2004; McNaughton, 1979; Putman, 1986). Another indirect effect influencing community composition is the alteration of the water balance. Reduced biomass may reduce the area of transpiring leaves, exposing areas of the soil. This increases the drying influence of wind and sun (Crawley, 1983; Putman, 1986).

It is clear that herbivores exert significant effects directly upon the vegetation itself. Moreover, they also create a whole series of indirect "knock-on" effects. The various effects of herbivory, rooting and trampling results in modification of the habitat and the environment offered to other organisms. For example, changing the physical structure of the habitat results in a modified microclimate. This modified microclimate will influence the animals and secondary plant species that can colonize this modified environment. Thus, the changes in structure, productivity and community composition that the herbivores cause within vegetation, has at once additional impacts on the rest of the communities depending on the vegetation (Putman, 1986; Vázquez, 2002). If such changes in community composition caused by the presence of herbivores continue over a protracted period, real shifts in community structure may be observed. Even conversions of an entire community type to another are possible (Putman, 1986).

2.1.2 Wild boar rooting and impact on plant communities in temperate forests

As said before, deciduous forest forms the preferred habitat in our region (Brunet et al., 2016; Fonseca, 2008; Welander, 2000b). Forest herbaceous ground cover is a very important part of forest biodiversity. Understory species may account for 80% of all forest plant species (Abbate et al., 2015; Gilliam, 2007). This understory vegetation is also an important component of wild boar's diet in temperate forests. Therefore, this ecosystem component is perhaps the most convenient for research on the impact of wild boar on temperate forests (Cuevas et al., 2010; Pinna et al., 2007; Sandom et al., 2013). These forests know a strong seasonal variation in understory vegetation. Shade avoiding ephemerals occur in spring, followed by shade-tolerant shallow growing perennials in summer and light demanding taller herbs in canopy gaps (Bruinderink & Hazebroek, 1996; Brunet et al., 2016; Fonseca, 2008; Geptner et al., 1988; Goulding et al., 1998; Welander, 2000b). Herbivory pressure in the understory is hard to detect. Often the whole plants are consumed or die, leaving no direct sign of herbivory. Instead, impacts are often only noticed on longer timescales. To examine these impacts, like reduced abundances and reductions in height and number of reproductive plants, often years of vegetational data is needed (Anderson, 1994; Augustine & Frelich, 1998; Frerker et al., 2013; McGraw & Furedi, 2005).

Examples of comprehensive studies with the goal of examining the environmental impact of wild boar on plant communities in temperate forests are limited, especially in its native range. Studies that are present show that impacts can be severe. Decreases up to 80-95% of ground herb cover are observed. Indicating that wild boar can threaten the regional occurrence of plants (Bialy, 1996; Brunet et al., 2016; Falinski, 1986; Wirthner et al., 2012). In non-native areas, wild boar invasion into forest communities often results in the replacement or even the removal of the understory (Aplet et al., 1991; Mack & D'Antonio, 1998; Russell-Smith & Bowman, 1992).

The specific effects of wild boar rooting on understory vegetation consists of both direct and indirect mechanisms. Direct impacts include direct feeding on seeds, bulbs, tubers, roots and rhizomes. Also uprooting of plants and mechanical damage caused by rooting for other food sources can be seen as direct effects. Indirect effects are zoochorous (endo- and epizoochory) dispersal of seeds, changes in soil properties and changes in interspecific plant competition mechanisms (Brunet et al., 2016; Burrascano et al., 2015; Cushman et al., 2004; Wirthner et al., 2012). Through these impacts it is expected that rooting will facilitate some understory species and detriment others. Species that are adapted to mechanical damage and or to herbivory will be favored. For instance, the composition of woody understory can be altered trough the selective herbivory on large-seeded species. In temperate forests most large seeded species or ether shrubs or trees, therefore wild boar feeding can have negative effects on these shrubs and trees (Burrascano et al., 2015; Siemann et al., 2009). Favoring certain woody species over others on a long time-scale can lead altered successional trajectories of a forest stands (Nuttle et al., 2014). On the other hand, mechanical damage may favor clonal species. Clonality can allow for a rapid recolonization of uprooted patches. This can lead to the development of a plant community dominated by a long-lasting layer of browse-tolerant species and ferns. This disturbance can even delay or suppress the recovery of plant species after the cessation of the disturbance (Burrascano et al., 2015; Catorci et al., 2012; Nuttle et al., 2014; Royo & Carson, 2006). Thus, foraging, and rooting activity of wild boar can thoroughly change the composition and abundance of understory species. Thereby, influencing ecosystem functions and services (Gilliam, 2007).

Brunet et al. (2016) analyzed permanent plots in a temperate deciduous forest in Sweden before and after the return of wild boar. Wild boar got extinct in Sweden during the 17th century and returned in 1970. This return was followed by a rapid increase in wild boar density (Thurfjell et al., 2009). In this study they quantified the effects of wild boar rooting on ground layer cover, species richness and species composition. They found that rooting can increase the general species richness of the herbaceous layer in the short-term. Main drivers are increased zoochorous seed dispersal and increased plant recruitment caused by rooting. Rooting created good soil and light conditions for seedlings. Rooting also resulted in a more heterogenous vegetation pattern. However, they also found that rooting can greatly reduce ground cover of spring ephemerals, threatening their associated ecological functions. Stronger reductions were found in plots with highest rooting intensities. Similar effects were found by Bialy (1996) and Howe (1981). Mean cover of summer green was not altered by rooting, probably due to less rooting in summer since agricultural crops form an important part of their summer diet in this study area.

Burrascano et al. (2015) also studied the relation between rooting intensity and vascular plant understory. They looked at the effects of rooting in a Mediterranean deciduous forest in Central Italy. They examined the effects on species composition and diversity. Further, they also examined which functional (response) traits are associated with different rooting intensities. They found an effect of rooting on the composition and dominance of plant species in the herbaceous layer. Selective feeding and the creation of disturbed areas which can get colonized by some species are the main reasons for this effect. No significant difference in species richness was found. They expected that some understory species will be favored by rooting due to their life-history traits and ecological requirements. For example, clonal species like ferns or other species that can recover quickly like *Poa sp.* may be favored (Catorci et al., 2012; Groot Bruinderink & Dekker, 2010). Part of their results on species functional traits were however unexpected. But these could get explained by long-term biological legacies of past wild boar rooting. The low intensity rooting areas used in this research have been rooted heavily in the past. Functional traits store information of the past disturbance history of a stand (Burrascano et al., 2015; Paušič & Čarni, 2013).

Another study about the ecological impacts of wild boar rooting was done by Sims (2006). Among other things, the effect of rooting at the community level was examined in East Sussex (England). Three disturbance regimes were studied: (1) unrooted areas (control), (2) rooted areas that were fenced after initial rooting (single rooting events), and (3) unfenced rooted areas. Since wild boar tend to re-root in the same area (Bruinderink & Hazebroek, 1996; Falinski, 1986; Goulding, 2003; Sims, 2006), this third treatment represents potentially frequent rooting events. Sims (2006) hypothesized that effects within two months of rooting would decrease percentage cover and species richness. On a longer timescale, between two and seventeen months after disturbance, it was expected that single or annual rooting by wild boar (treatment 2) would lead to an increased cover and richness. Increased levels of soil nutrients and good seeding beds can have a positive effect on plant cover and species richness. Repeated rooting (treatment 3) was expected to decrease both cover and richness. These hypotheses are in line with the intermediate disturbance hypothesis (Connell, 1978). High and or frequent disturbance will lead to low species diversity, richness, and evenness. Intermediate disturbance, for example annual rooting, is known to maximize diversity and species richness. Indicating the crucial role that rooting can play in the community composition. Rooting leads to exposure of the seed bank and can affect in this way re-establishment of the present plant community. This exposed seed bank can also lead to an alteration of the size and structure of the plant community (Kotanen, 1995). Also, quick colonizers, therophytes (annuals) and regenerating survivors are likely to benefit from rooting (Kotanen, 1995; McIntyre et al., 1995; Sims, 2006; Welander, 2000a). A shift to less ancient woodland indicator species (AWI) in rooted plots was also predicted. AWI have low dispersal potential and are characterized by a stress tolerant strategy (Hermy et al., 1999; Wulf, 1997). Thus, they are not adapted to coping with severe wild boar disturbance regimes.

As hypothesized, total plant cover was indeed greater in single rooted plots than in unrooted and multiple rooted plots. Also, the plant species richness and the Shannon Diversity Index were significantly greater in rooted than in non-rooted plots. This was again higher in single rooting plots than in the multiple rooting plots. There were no significant effects of rooting found on the presence of AWI species (Sims, 2006).

Wild boars are or were a natural component of many forest ecosystems in Europe. Positive impacts of wild boar like increased plant recruitment and seed dispersal can increase overall species richness. However, long term frequent disturbance or too great disturbance regimes may cause degradation of forest herb layers and cause local extinctions (Bratton, 1974; Brunet et al., 2016). Impacts of large omnivores and herbivores are positively related with their density (Nuttle et al., 2014). Therefore, it is clear that their recent increase and local overabundance can have negative effects. Reducing the frequency and abundance of rooting disturbance can be needed in areas with high population densities, therefore local population control of wild boar and other ungulates can be crucial.

2.1.3 Density dependent tipping points

As said before, the impacts that ungulates exert on their environment depends on the density. Population density, together with local abiotic and biotic conditions, forest management and browsing intensity, determines whether ungulates have a beneficial or harmful impact on their environment (Heckel et al., 2010; Pellerin et al., 2010; Ramirez et al., 2018; Van Hees et al., 1996). In line with the intermediate disturbance theory (Connell, 1978) it is expected that at a certain ungulate density shifts to undesired states are possible. Therefore, it is needed to understand wild boar, and other ungulates, density related impacts. So that we may be able to determine critical tipping points. On these tipping points population density starts to have detrimental impacts on forest ecosystems. Whether impacts are neutral, positive, or negative can be determined with dose-response curves. The shape and the lag times of these curves can be used to detect these tipping points (Nuttle et al., 2014; Ramirez et al., 2018).

In line with the intermediate disturbance theory of Connell (1978) we can make a hypothesis about a density dependent impact. At low ungulate densities we suspect a structural uniform and dense vegetation. This low heterogeneity in both habitats and light conditions predicts a low plant species diversity (Lucas et al., 2013; Ramirez et al., 2018). At intermediate ungulate densities forest undergo higher vegetation removal, soil disturbance and seed bed preparation. This results in a higher habitat heterogeneity. Also selective feeding, steering plant competition and succession, contributes to a higher species richness at intermediate disturbance regimes (Nuttle et al., 2014; Ramirez et al., 2018). At high ungulate densities, overconsumption, high rooting disturbance and high ungulate trampling results again in reduced species diversity (Ramirez et al., 2018; Schippers et al., 2014).

However, little is known about the shapes of these dose-response curves between forest attributes and herbivore density. Nor about tipping points and critical points (Putman et al., 2011; Ramirez et al., 2018; Reimoser & Putman, 2011). During my literature review no specific research was found addressing these questions about wild boars specifically. Ramirez et al. (2018) assessed the impacts of ungulate density on forest development, functioning and regeneration. For this they carried out a literature review of 433 studies in temperate forests. Combining the data of these studies to model dose-response curves of the effects of ungulate density on forest structure, functioning and tree regeneration. They found critical tipping points where ungulate densities started to be detrimental for the forests. These densities are expressed as ungulate metabolic weight densities (kg/km^3). This method enables them to combine the assessment of multiple ungulate species. For forest structure a critical tipping point of 141 kg/km^3 was found. For forest functioning the metabolic weight density at tipping point was 251 kg/km^3. And for forest regeneration a tipping point at 115 kg/km^3 was found. These metabolic weight densities are respectively equivalent to 5.2 wild boars per km^2 for forest structure. 9.4 wild boars per km^2 for forest functioning. And 4.3 wild boars per km^2 for forest regeneration. Forest functioning is clearly least sensitive to ungulate disturbance. However due to time lags these effects may build up over time and become negative as well at lower densities. These tipping points are also likely to be lower in less fertile systems and higher in more fertile systems (Cromsigt & Kuijper, 2011).

Ramirez et al. (2018) also fitted the dose-response curves to check the response of forest structure, forest functioning and forest regeneration to ungulate density (figure 9). In general, we can see that effects are more negative with increasing ungulate density. According to their results the dose-response curves are sigmoidal declining, and not unimodal as would be expected by the intermediate disturbance theory (Connell, 1978). This indicates that effects changed from neutral to negative with increased ungulate density. Thus, no optimal ungulate density for a positive effect on forest attributes was found. The dose-response curves consist of a gradual decline with increased ungulate abundance, followed by a steep decrease.

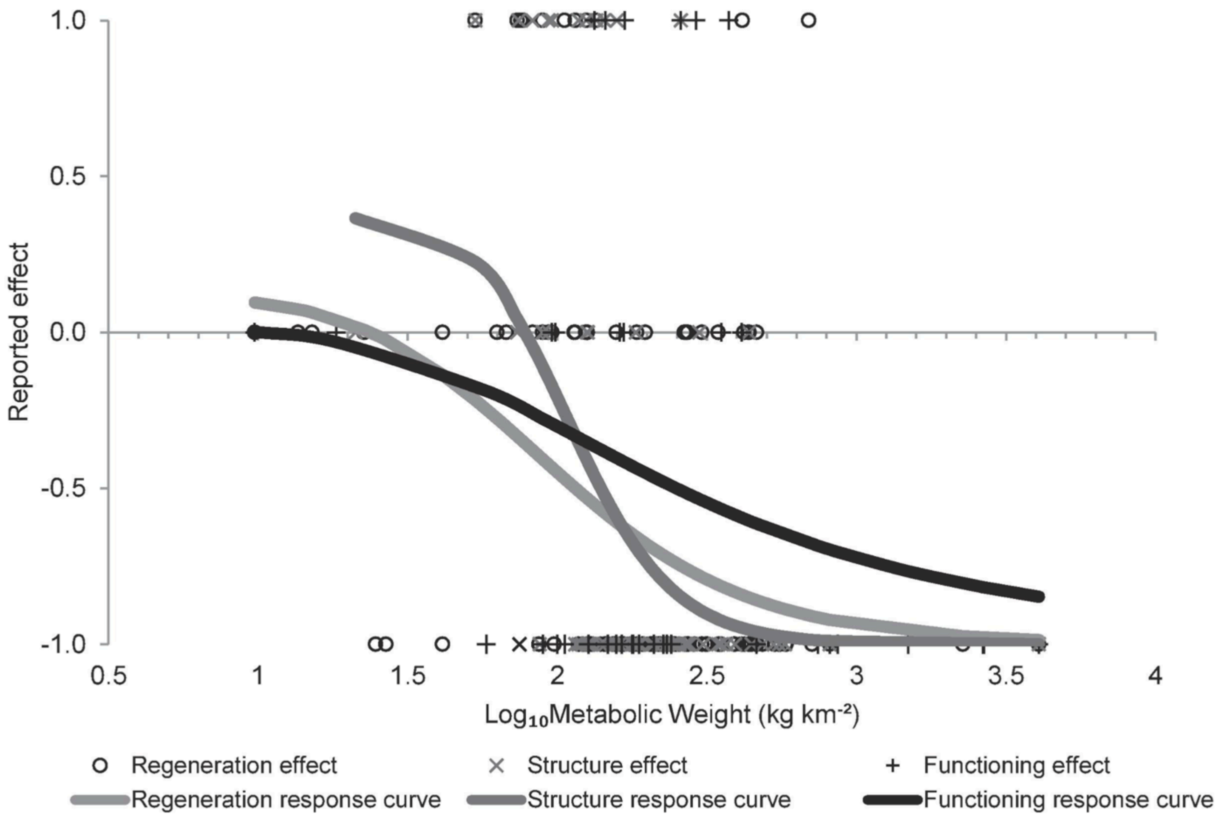


Figure 9: Dose-response curves between metabolic weight density (kg/km3) and the probability of studies reporting a significantly (1) positive, (-1) negative or (0) neutral effect. Dose-response curves are given for forest regeneration (light grey), forest structure (dark grey) and forest functioning (black).

2.2 Impacts on fauna

Figure 10 gives a graphical overview of some impacts wild boar can exert on animals according to Massei & Genov (2004). Impacts can again be both positive and negative. Often depending on the amount of disturbance and thus of the wild boar density. A direct impact can be predation. Since they are opportunistic feeders and their diet is mainly plant based (± 90%), this impact is normally not very great. Indirect effects on vegetation and soil structure, through for example rooting, can lead to the increase or decrease of animals depending on the species requirements (Ballari et al., 2015; Groot Bruinderink & Dekker, 2010). The effects on animals are in general largely unexplored, specifically in native ranges (Barrios-Garcia & Ballari, 2012)

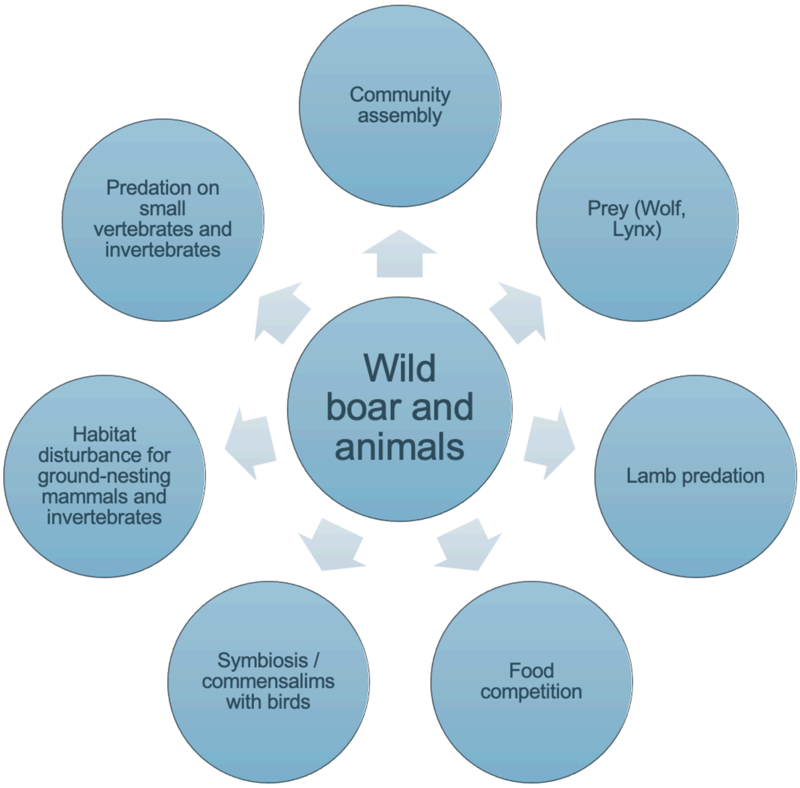


Figure 10: Impacts of wild boar on fauna. Adapted from Massei and Genov (Massei & Genov, 2004)

Sometimes predation by wild boar can have positive effects in our way of viewing. For example, when preying on pest species larvae, damage caused to commercial tree plantations by this pest species can be decreased (Leaper et al., 1999; Massei & Genov, 2004). They can also be an important source of prey for large predators. However, this is in our case not very meaningful since the wolf (*Canis lupus*) and the lynx (*Lynx lynx*) only very recently returned to Belgium. Also symbiosis of feeding/cleaning with corvids are observed (Barrios-Garcia & Ballari, 2012; Massei & Genov, 1995).

High density of wild boar populations can damage the structure of faunal communities (Carpio et al., 2014). In some cases, predation by wild can have large impacts on invertebrate abundance. This can lead to a decrease of macro-invertebrates in the soil. Also, a decrease of ground nesting birds due to predation of eggs and birds occurs (Casaer & Van Den Berge, 2006; Massei & Genov, 2004; Tack, 2018). Negative effects of predation on small ground dwelling mammals and ground nesting birds can be indirectly enhanced by rooting due to habitat destruction (Massei & Genov, 2004). Predation on insects can also lead to food competition with other small insectivores. However, this is highly versatile between species

(Singer et al., 1984). We found no specific studies that specifically quantified diet overlaps between other animals and wild boar, but it is suggested that food competition between other mammals and wild boar is likely (Massei & Genov, 2004; Massei et al., 1996; Singer et al., 1981). It is known that due to their large impact they can restructure or alter entire food webs. Predation on domestic animals like lambs also occurs, but is only limited and mainly occurs in introduced ranges (Choquenot et al., 1996; Massei & Genov, 2004).

3 Research gaps

Many studies found in literature indicates that excessive numbers of wild boar, and other ungulates, can exert a considerable impact on fauna and flora. These impacts can form a significant threat to temperate forests (Massei & Genov, 2004; Rackham, 2008). Although, this being of prominent and growing concern, there are limited numbers of good quantitative scientific studies on the relationship between wild boar and forest biodiversity. The lion’s share of these studies was done in introduced ranges. Less studied are the native ranges where also a spread in both abundance and distribution is observed. Most of the available papers show no clear significant relationships between the presence of wild boar and biodiversity. Relationships found are either positive, negative, or non-existing. Knowledge gaps of their environmental impacts and how they can alter ecosystem functions and processes still exist (Barrios-Garcia & Ballari, 2012; DEFRA, 2008a).

A main gap is the relation between impacts and wild boar densities. In agreement with the intermediate disturbance hypothesis (Connell, 1978) we can suspect density dependent impacts. Therefore, there is need for research determining possible tipping points. From which wild boar density does the impact become negative? This question is complex and the answer will be dependent on parameters like the local species pool, the local environment, the local climate, management goals, fertility of the system, habitats, habitat conditions and herbivory history of the habitats (Barrios-Garcia & Ballari, 2012; Ramirez et al., 2018). For this to happen, specific monitoring protocols that examine the effects of absence/presence and changing densities of wild boar is needed (Fagiani et al., 2014). However, at the moment often wild boar density estimations are not very accurate and reliable (Consortium et al., 2018), making the study on the impacts on vegetation complicated.

Therefore, there is a need for additional research to get a better idea of the impacts they exert on the environment. For the detection of biologically relevant changes in diversity of both faunal and floral communities, statistically robust monitoring protocols are essential (Fagiani et al., 2014). As said, impacts can vary between different habitats, habitat conditions and between native and introduced range, indicating that thorough examinations are necessary (Barrios-Garcia & Ballari, 2012). Their vast increase, more or less worldwide, enhances this need for additional research. Without this, good and sound management plans, aiming at eradicating or controlling wild boar, cannot be constructed (Massei & Genov, 2004).

Goals

Wild boar populations have grown substantially in recent years (Pfaff & Saint Andrieux, 2007; Sáaez-Royuela & Telleriia, 1986; Wirthner et al., 2012). Their population expansion in both area and abundance have led to increased impacts. Especially its rooting activity can mediate profound ecological effects (Brunet et al., 2016; Burrascano et al., 2015). The most suitable ecosystem component for wild boars in temperate forests is the understory vegetation (Cuevas et al., 2010; Pinna et al., 2007). The understory vegetation is also a very important part of the forest overall biodiversity, accounting for up to 80% of plant species (Abbate et al., 2015; Burrascano et al., 2015; Gilliam, 2007). Making the understory vegetation a fitting component for a study on the impacts of wild boar.

However, currently most research on the impacts of wild boar focusses on damage to agriculture and on its effects on tree regeneration (Barrios-Garcia & Ballari, 2012; Gómez & Hódar, 2008; Ickes et al., 2005; Schley & Roper, 2003). More recently some studies also focused on the effects of rooting on the forest understory vegetation (Brunet et al., 2016; Burrascano et al., 2015; Sims, 2006). The goal of this study is to contribute knowledge about wild boar disturbance on the vegetation development in a temperate forest. Gaining new insights for a consensus on the effects of rooting on the understory species composition and richness. In this way future management can be adapted to recent developments regarding the presence of wild boar.

The goals and accompanying research questions can be divided in two parts, respectively a 1) non-temporal and a 2) temporal part:

1) Examining the relationship between specific habitat parameters, plant functional traits, plant species and plant communities and wild boar rooting intensity. In order to get an undisturbed idea of this relationship, we will look at the link between current wild boar rooting intensity (2020) and field variables prior to wild boar recolonization (2003-2005). Specific research questions are:
    - Is there a spatial pattern in wild boar rooting intensity?
    - Does wild boar prefer plots with specific soil, dendrometric and plant functional traits characteristics for rooting?
    - Are there particular plant species or plant communities with more wild boar activity?

2) Examining the impacts of recent wild boar recolonization and different levels of rooting intensity on the understory vegetation development in the Meerdaal forest. Here we use and compare detailed vegetation data gathered in permanent plots for three time periods: before recolonization of wild boar (2003-2005), after recolonization but still low wild boar densities (2013-2016) and after recolonization and increased wild boar densities (2020). Specific research questions are:
    - Does wild boar rooting disturbance lead to a shift in total plant cover, species richness and species diversity through the years?

- Does wild boar rooting disturbance lead to a shift in species functional traits through the years?
- Does wild boar rooting disturbance favor or disfavor some plant species?
- Does wild boar rooting disturbance lead to a shift in herbaceous understory community composition through the years? Are these differences larger in plots that are assumed to be rooted more frequently through the years?

Materials and methods

1 Study area

The Meerdaal forest, with an area of about 1.600 ha, is one of the largest forest complexes in Belgium (Baeten et al., 2008; Baeté et al., 2004). It belongs to the provinces of Flemish Brabant and Walloon Brabant (figure 11). It is situated in Central-Belgium, east of the Dyle valley and just a few kilometers south of Leuven. The largest area of its public part is located in Flanders (ca. 1255 ha), only 64 ha of public area lays in Walloon Brabant. Currently the forest complex is mainly surrounded by agricultural fields, small private forests and built-up area (Baeté et al., 2004).

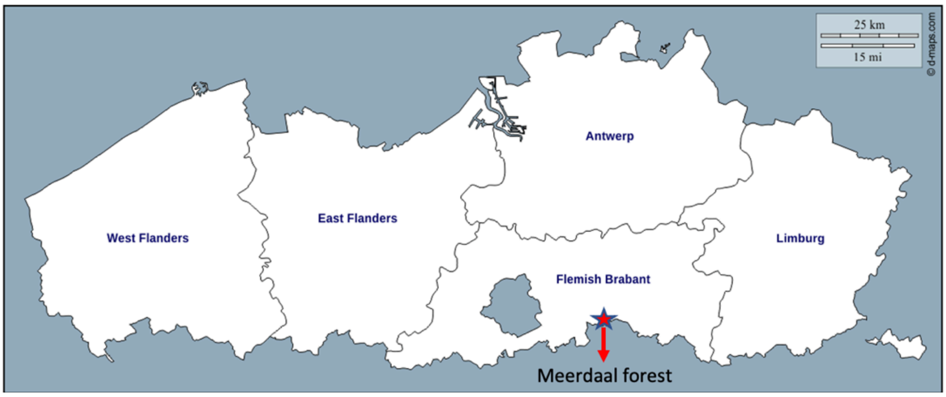


Figure 11: Position Meerdaal forest in Flanders. Adapted from d-maps.com.

Since 1995, a part of the Meerdaal forest (187.5 ha) is classified as forest reserve: “bosreservaat Meerdaalwoud” (figure 12). It contains the sub-areas Everzwijnbad, Pruikenmakers, Grote Konijnenpijp, Veldkant van de Renissart, Drie eiken, Mommedeel and De Heide (Baeté et al., 2004; Baeté et al., 2007). In 2000 these forest reserves gained the statute of integral forest reserve. Since then, a zero-management strategy is applied. However, prior 1995 regular forestry practices were applied here (De Keersmaeker et al., 2009; Meuleman, 2006). The forest reserve is owned by the Flemish Region and is managed by the “Agentschap voor Natuur en Bos” (Baeté et al., 2007).

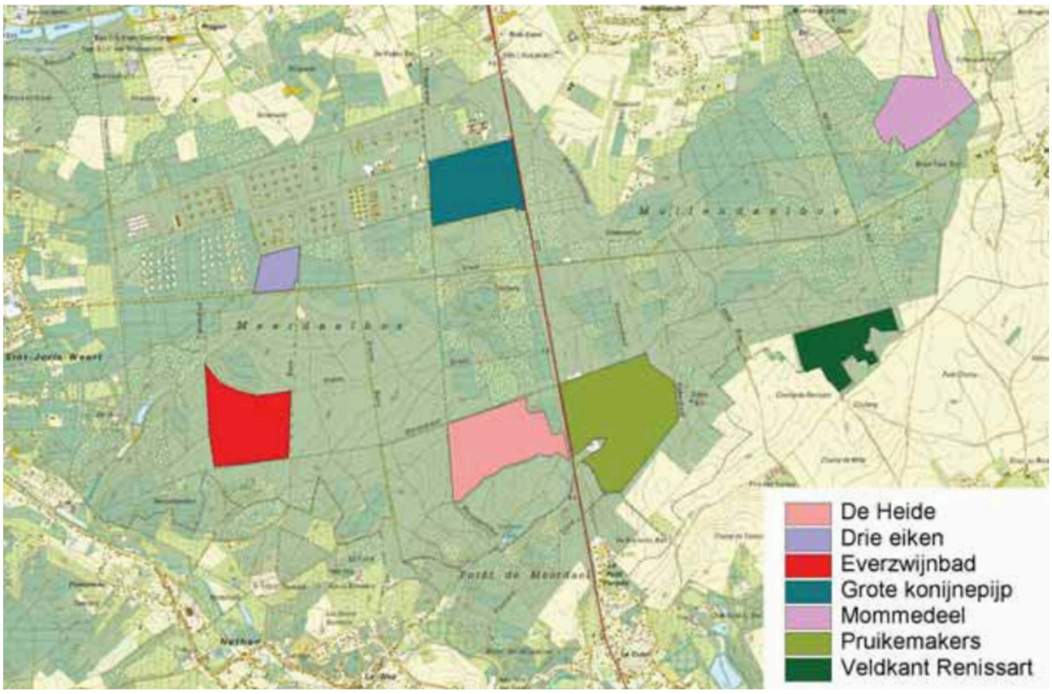


Figure 12: Sub-areas of the forest reserve in Meerdaal forest (Baeté et al., 2004).

This study has been conducted in the sub-areas Everzwijnbad and Pruikenmakers of the forest reserve, they lay approximately 2.5 km apart (figure 12). The sub-area Everzwijnbad has an area of 27.5 ha, Pruikenmakers has an area 48.6 ha (Baeté et al., 2004; Baeté et al., 2007). Both areas are embedded in the larger forest complex, which is managed through small-scaled harvest interventions.

Both sites compromise of mixed, uneven, highly structured, closed-canopy stands of broadleaved forest (for details: see chapter Materials and method: part 1.8 Vegetation).

1.1 Wild boar in Meerdaal forest

As mentioned in chapter “1.2 Distribution in Belgium”, wild boar was probably present in high densities in the larger forested areas in both Wallonia and Flanders until the end of the eighteenth-century (Casaer & Licoppe, 2010). According to Baeté et al. (2009), the former landowner of the Meerdaal forest and Heverleebos, duke Lodewijk Engelbert d’Arenberg (1750-1820), was a big fan of wild boar for hunting. When emperor Joseph II created the Imperial ordinance (1781) which forbade the free roaming of wild boars throughout the Austrian Netherlands, duke Engelbert opposed against this obligation. His plan was to herd the wild boar of the Meerdaal forest into the walled area of the nearby Carmelite monastery of Savenel. How many animals that have roamed in these sacred gardens is unknown. We do know that Savenel’s wild boars were culled in 1790 by 35 armed volunteers in service of the United Belgian States (Baeté et al., 2009). Since then, as for the rest of Belgium, wild boar and other ungulate species populations declined due to poaching and bad management during several wars and revolutions.

The most recent culling of wild boar in the twentieth century dates from 1957. During this year the last known individuals were shot in Meerdaal forest. Between 1958 and 2008 virtually no wild boars were observed in Flemish Brabant (Meuleman & Vanwanseele, 2019). Only during harsh winters infrequent observations of solitary animals from Walloon populations were made (Baeté et al., 2007; Janssens et al., 2004; Meuleman, 1998). Similar like for the rest of Flanders, in the last two decades a return of wild boar has been observed in the Meerdaal forest. During 2004-2005 a 60m wide wildlife crossing, named “De Warande”, has been built over the Naamsesteenweg in the Meerdaal forest. Since then, the use of this crossing by animals has been monitored periodically (Baeté et al., 2007; Lambrechts, 2010; Lambrechts et al., 2019). During the first observation period in 2006 multiple observations of an individual wild boar were made on this wildlife crossing (Baeté et al., 2007). The second observation period in 2008 only resulted in one individual sign of presence of wild boar (Lambrechts, 2010). However, in 2012 the wildlife crossing was monitored again. During this effort it was found that wild boar was no longer a rarity for this region (Lambrechts et al., 2019). In 2016, the first sucklings were observed by the local foresters, proving local reproduction. As of 2016, there is an established population of an estimated of 100 animals (Meuleman & Vanwanseele, 2019). The animals probably migrated northwards from Wallonia to the Meerdaal forest, Heverleebos and the Dyle valley.

Since 2006 Instituut Natuur- en Bosonderzoek (INBO) collects, processes, and presents all known hunting statistics of big game within the Flemish region (grofwildjacht.inbo.be). All data and figures can be freely used and downloaded. Figure 13 gives the total hunting statistics for the Flemish Region and the detailed data from the municipalities Bierbeek and Oud-Heverlee. These municipalities encompass the Flemish part of the Meerdaal forest. Since it is impossible to determine the exact number of wild boars, estimates based on the culling data are important proxies to gain insight into estimates like the minimum population. We can see on figure 13 that since 2006 the number of shot wild boar in Flanders has increased from 1 to 2349 individuals, with a stable period between 2012-2015. From 2016 onwards the increase is almost exponential. The same trend is measured for the combined hunting data of Bierbeek and Oud-Heverlee. Prior to 2015 no animals were killed, after 2015 the number of shot wild boar has increased to 52 in 2019 and 50 in 2020.

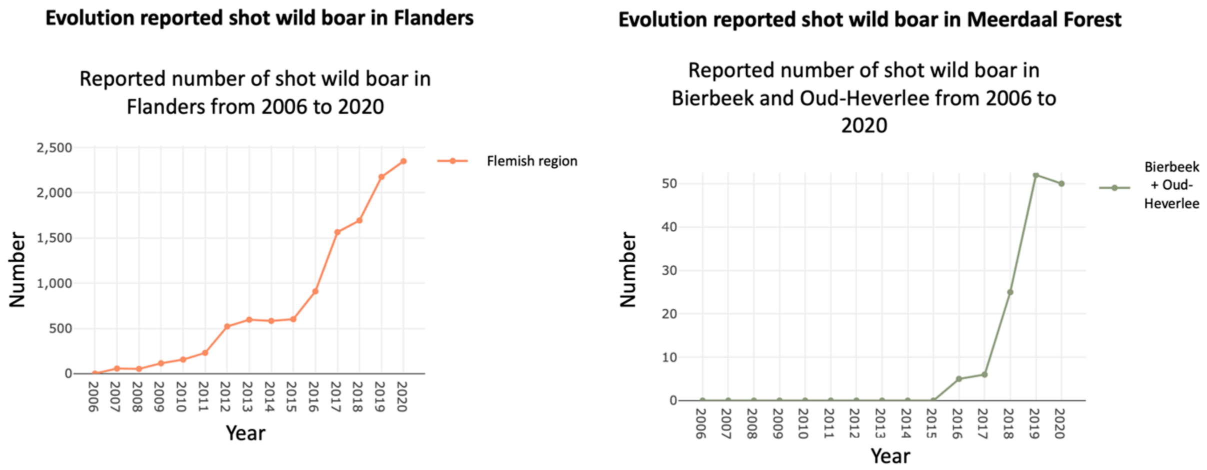


Figure 13: Reported number of shot wild boar per year (2006-2020) in Flanders and in the Flemish part of the Meerdaal forest (Bierbeek and Oud-Heverlee). Source: grofwildjacht.inbo.be

1.2 Climate

The Meerdaal forest has a humid mesothermal climate with a small water deficit according the Thornthwaite climate classification system. This results in a moderate and mild oceanic climate. This climate allows a good development of vegetation during 6-7 months per year, from April-May until October (Baeté et al., 2004). Weather measurements of the weather station at Ukkel can be used for the Meerdaal forest (www.kmi.be). This station is only 25km away from our study area and is located at more or less the same height above sea level (ca. 100m). Figures 14 and 15 give respectively the monthly climate normals of temperature and precipitation for the time periods of 1961-1990, 1971-2000, 1981-2010 and 1991-2020. On figure 14 it is clear that the temperature has slightly increased during the last decades. For the precipitation no clear trends can be observed (figure 15). The most recent (1991-2020) data gives a yearly average temperature of 11°C and a yearly average precipitation of 837.1 mm. The temperature reaches a clear optimum in the summer months (figure 14), the precipitation however is evenly spread over the entire year (figure 15). The potential evapotranspiration of a forest in this climate zone is 600 mm according to Sanders et al. (1985). This means that there is a yearly rainfall surplus from ca. 250mm in the Meerdaal forest. This results in a leaching climate, which has a crucial impact on nutrient availability for plants and soil development (Baeté et al., 2004).

According to the KMI, the dominant wind direction blows from the west. Geebelen (1963) states that the dominant winds come from the south-west, especially during autumn and winter.

Northeastern winds mainly occur in April-May. Further, early and late frost is not frequent (Baeté et al., 2004).

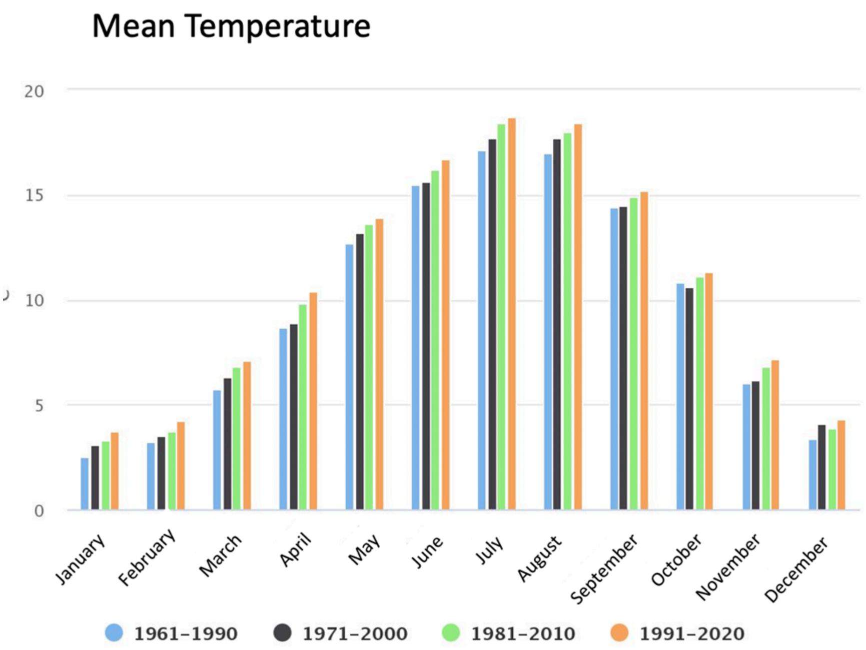


Figure 14: Mean monthly temperatures in Ukkel for 1961-1990, 1971-2000, 1981-2010 and 1991-2020 (Konklijk Meteorologisch Instituut (KMI))

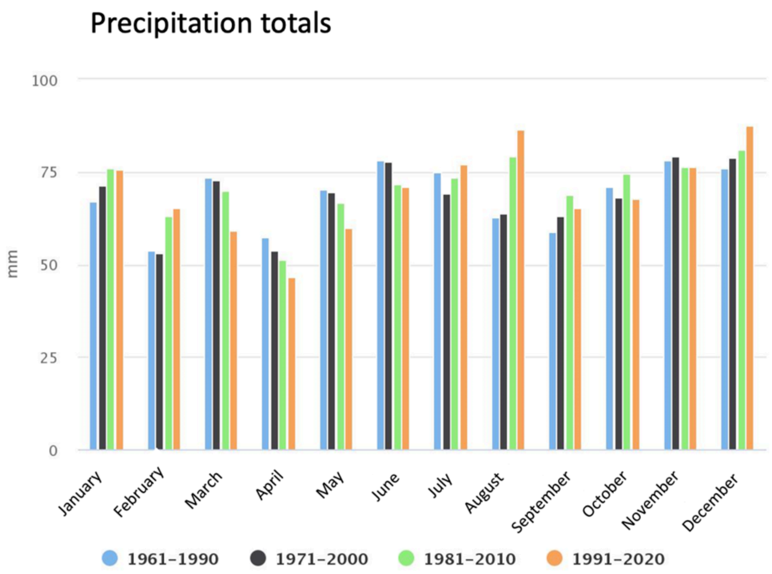


Figure 15: Mean monthly precipitation in Ukkel for 1961-1990, 1971-2000, 1981-2010 and 1991-2020 (KMI)

1.3 Topography

The Meerdaal forest is situated mainly on a hilly loess plateau, varying between 35 and 103 meters above sea level. Local slopes up to 25% can occur, though mainly weak slopes are dominant. The forest reserve Everzwijnbad slopes down towards the northwest and situates between 90 and 60 meters above sea level. In the northwestern part a slope of more or less 5% is present. The southern part is characterized by a slope of only 2% (Baeté et al., 2004). The forest reserve Pruikenmakers has a height between 57 and 93 meters above sea level. A valley, going from the northwest towards the southeast, is present in this forest reserve. Branching of this valley in the southern part is characterized by deep incisions with steep slopes (figure 16).

Figure 16: Deep gully formation at plot 922 in the southern part of forest reserve Pruikemakers. Picture: Hendrik Willems

1.4 Soil and hydrology

Mainly well drained, loamy soils that are leached out by the precipitation surplus are present at the Meerdaal forest. The main soil types are luvisol and albeluvisol according to the FAO classification (Baeté et al., 2004). The soil map of Belgium show that the forest reserve Everzwijnbad (figure 17) almost entirely consists of well drained, acidic, loamy soils (classification Abc0 en Aba(b)). A small part a the southeastern edge is characterized by a more sandy soil classified as a well-drained, acidic sand-loam soil (sLbc) (Baeté et al., 2004). The soil types at forest reserve Pruikenmakers are more diverse (figure 18). Dry, loamy and sandy soils, as well as humid to wet loamy soils are present (Baeté et al., 2007). No surface water are seepage zones are present, the permanent groundwater table is located at more than 5 meters of depth (Baeté et al., 2004).

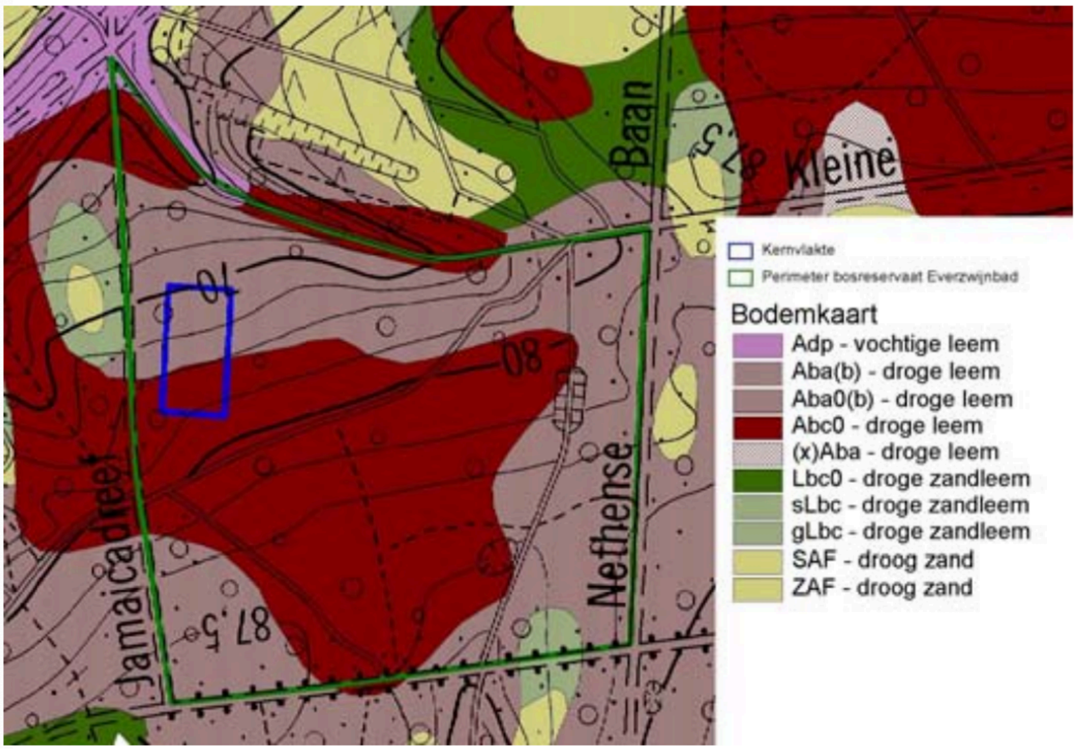


Figure 17: Soil map of Belgium, detail of Everzwijnbad (Center for Soil mapping)

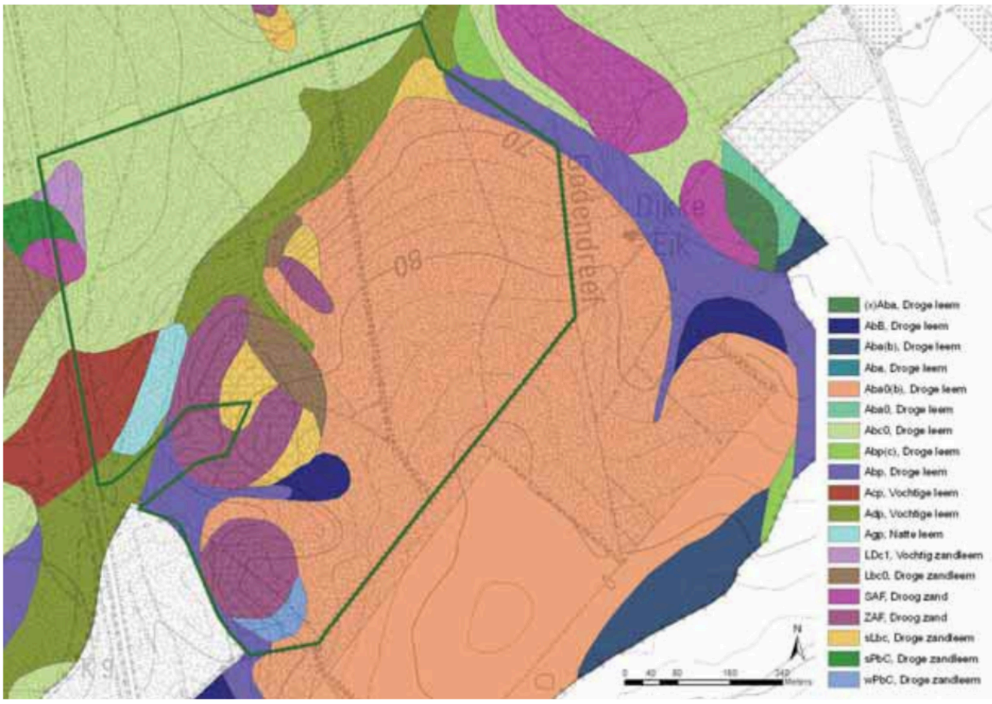


Figure 18: Soil map of Belgium, detail of Pruikenmakers (Center for soil mapping)

1.5 Property history

The Meerdaal forest is a large forest complex. According to our knowledge, it has always existed (De Keersmaeker, Baeté, et al., 2005). However, some evidence suggests that parts of the forest has been used for agricultural practices in the Gallo-Roman period (De Keersmaeker et al., 2009; Roger Langohr, 2008; Vanwalleghem et al., 2004). Up until the 13th century it was property of the dukes of Brabant. After 1338 it became in possession the Norman Harcourt family, later (1432-1440) followed by the Cröy family. The marriage between Anne de Cröy and Charles d'Arenberg (1616) changed the possession to the Arenberg family. After the first World War all possessions of the German Arenbergs became under Belgian sequestration. In 1929 the forested domains of the Arenberg family (Egenhovenbos, Heverleebos and Meerdaal forest) became property of the Belgian state (Brichet, 1938; De Keersmaeker, Baeté, et al., 2005; Geebelen, 1963).

1.6 Land use and management history

This section is based on the basis reports of forest reserve Everzwijnbad and Pruikenmakers by Baeté et al. (2004; 2007) and the monitoring reports of forest reserve Everzwijnbad and Pruikenmakers by De Keersmaeker et al. (2005; 2009).

1.6.1 Land use history

Currently, the oldest archeologic finds in the Meerdaal forest date from the Neolithic period (6500-4000 year ago). So far, no archeological discoveries can be dated with certainty to the Paleolithic or Mesolithic Age (De Bie, 2003). The most important discoveries were found in a radius of approximately 1km around forest reserve Pruikenmakers. These Neolithic findings are mostly work tools made of polished flint stones (Adriaenssens, 2007). Numerous axes were found, insinuating that the Neolithic residents were already actively intervening in the forest stock by cutting and ring-barking trees (De Bie, 2003). Older findings date from the Iron Age. A few km from Pruikenmakers and Everzwijnbad, on the plateau of Saint-Nicasius, remains of a defense with an earthen rampart was found. Near this rampart, also six pre-Gallo-Roman burial mounds are found (De Bie, 2003).

The Meerdaal forest is also characterized by the occurrence of anthropogenic incisions. These were already mentioned in literature in the beginning of the 21st century (Vincent & Vincent, 1909). Based on their morphology, these anthropogenic gullies can be divided in two groups (Vanwalleghem et al., 2003a; Vanwalleghem et al., 2003b). The first group is mainly found in the south of the Meerdaal forest. Suspected is that these are not the result of rain, but the result of past arable farming practices (Vanwalleghem et al., 2003b). Due to the lack of Merovingian or medieval sites, it is suspected that the period of farming in the Meerdaal forest ended after the attacks of the Franks (275 AD). The second group of incisions are mainly located along straight, north-south oriented axes. These are presumably remains of former roads. Some of these gullies are located in Everzwijnbad and in the north of Pruikenmakers. The N-S oriented sunken lane in the eastern part of the forest reserve Everzwijnbad is believed to be an ancient Roman road. The WNW-OSO incision in the extreme northeast of Everzwijnbad is presumably part of the “Tiense Groef”, another ancient Roman road (Vanwalleghem et al., 2003a; Vanwalleghem et al., 2003b). Pruikenmakers is also characterized by a circular depression. This depression, as well as similar ones in the Meerdaal forest, is of anthropogenic origin as well. According to Vitse (2003) these depressions are the result of mining for calcareous loess that has been used for agricultural practices. Langohr (2008) suggests, however, that these depressions are the result of mining for decalcified loam used for bricks and pottery.

It is not certain that there was habitation in the Meerdaal forest during this Gallo-Roman period. However, several Gallo-Roman artefacts and concentrations of roof tiles suggest the presence of “villae rusticate” or other buildings (Adriaenssens, 2007; De Bie, 2003). Villae rusticae are small farms of 50-100 ha. According to Vanwalleghem et al. (2004), one such villae was situated at 1000 m from Pruikenmakers. Other evidence for the presence agriculture was found in 2008. In this study, a soil analyses was done in Pruikenmakers (Langohr, 2008). He found that a fragipan layer was lacking. This is a compact layer situated at approximately 35 cm depth. These layers got formed during periglacial times. The fragipan layer can be broken down due to human activity. Intensive forest grazing and conversion into meadows or agricultural field are listed as possibilities for the lack of this layer in the Meerdaal forest (Langohr, 2008).

According to Langohr (2008), the permanent presence of forest in the Meerdaal forest is highly unlikely. He states that the micro relief is strongly changed by anthropogenic influences. For example compared to the Sonian Forest, the increased bioturbation in the Meerdaal forest indicates long-term uses as agricultural fields or pastures. Also, large parts of the forest are flattened, a possible indication for former agriculture as well (Langohr, 2008). Prolonged plowing and spading levels out the relief. Another explanation for the flat relief is given though personal communication from Guido Tack to De Keersmaeker et al. (2009). Intensive coppice management was common for centuries in most forests, this management can have similar effects like agriculture on the relief. Especially, the excavation of roots for firewood can have a large impact. However, the high coverage and species richness of ancient wood plants in Pruikenmakers and Everwijnbad suggest that at least some areas in the vicinity were always forested (De Keersmaeker et al., 2009).

Little is known about the land use in the Meerdaal forest for the period between 300-1200 AD. A pollen research carried out by Munaut (1959) in the Warande, located in the vicinity of Pruikenmakers and Everzwijnbad, provides some information. The method used, however, is somewhat uncertain. And thus, the following resume of this study is therefore uncertain as well. According to the pollen record, the area was characterized by a grassy, open forest type with lots of hazel (*Corylus avellana*) during the Gallo-Roman period. This evolved towards a mixed, semi-open oak forest with heather (*Calluna vulgaris*) in the fourth until the fourteenth century. Later, in the fifteenth until the nineteenth century the area was forested with a closed oak-birch forest. This later evolved in a plantation dominated by oak and beech.

The Meerdaal forest got the title of “Vrijwoud” in 1367. Hunting in these forests is exclusively reserved for the monarch or the owners of these forests. In addition, in a non-manorial “vrijwoud” like the Meerdaal forest, the jurisdiction was reserved for the own legal system of the owners. In practice, this means that the “Vrijwoud” status was a protection against livestock farming, arable farming and habitation in these forests (Baeté et al., 2004).

The oldest known maps of the Meerdaal forest are precadastral card books that were made for Charles de Cröy, owner of the Meerdaal forest since 1595. Pierre de Bersacques made another drawing of presumably the same period (1596-1958). Both sources of information are however not easily interpreted. Together with other maps dating from 1597 of the surrounding forest, we can state with great certainty that since then the forest reserves Pruikenmakers and Everzwijnbad has been forested. An older map, a felling plan from 1723, shows that the land use has not been changed much since the period of Charles de Cröy. During the second part of the eighteenth century a big infrastructural change happened in the Meerdaal. The still existing road Naamsesteenweg was constructed. This road is still an important border of forest reserve Pruikenmakers (De Keersmaeker et al., 2009).

In the same century, between 1727 and 1770 the Meerdaal forest got divided according to a grid plan (Deneef, 2004). This plan divided the forest in several forest patches surrounded by straight roads. Pruikenmakers is still surrounded by the Walendreef (N), the Godendreef (E) and the Kanselierdreef (S). Everzwijnbad is surrounded by the Kleine dreef (N), the Nethense baan (E), the Walendreef (S) and the Jamaicadreef (W). The first document with the name Pruikenmakers dates from 1810. This map from Wirix shows a division of the forest complex in 34 sub areas. Topographical maps from 1865 and onwards show that the entire area of Pruikenmakers and Everzwijnbad is forested. Three coniferous plots are present on the maps of Pruikenmakers. After the first world war, the smallest and most northern coniferous plot got planted with deciduous wood (De Keersmaeker et al., 2009). During the last 150 years the forest land use did not change. However, during the two world wars felling of large trees was performed, especially in the coniferous parts. This resulted in large temporary clear-felled areas, replanted quickly after the felling.

1.6.2 Management history

The Brabant forests of Meerdaal, Mollendaal and Heverlee have had a good reputation among foresters for ages. An old document (1789) praising the forest management from the Arenberg family can be found in the book “Histoire des bois en forêts de Belgique” by Goblet d’Alviella (1930). Even in times of the Cröy family, owners of the Meerdaal forest before the Arenberg family, the Meerdaal forest was a forest with a very good reputation. Well managed forests with high quality logs were around 1600 a rarity in our regions. An acquittance dating from 1601 demonstrates the importance of the Meerdaal forest for building material. On this receipt we can see an order for the felling of 40 large oaks for the construction of the Cröy palace in Brussels. During this period, between the sixteenth and nineteenth century, the used management strategy was coppice-with-standards. Standards where mainly oak (*Quercus robur* and *Quercus petreae*) (De Keersmaeker et al., 2009; Vandekerkhove et al., 2021). The major management strategy remained coppice-with-standards up until almost 100 years ago. Rotation periods where between 12-14 years (Vandekerkhove et al., 2021)

The first regulations about the management in the forests of Meerdaal, Mollendaal and Heverlee, were already drawn up in 1557 and 1615. These documents already contain a full business scheme, detailed procedures, and management guidelines for the harvest sale of timber. Parts of these procedures are still comparable with the procedures used today (De Keersmaeker et al., 2009).

From the nineteenth/early twentieth century onwards the economic interests of coppice wood declined. At the same time the demand for heavy timber increased, leading to the slow conversion from coppice-with-standards to high forest. This transformation does not happen overnight, but it is of course the work from several generation of foresters. This led to a gradual conversion to oak high forest in Everzwijnbad and Pruikenmakers (Vandekerkhove et al., 2021). The coppice was no longer cut, leading to an increase in both the share and volume of standards. Also, beech trees became more popular due to their value as heavy timber.

Therefore, between 1850 and 1870 homogenous beech stands got planted in the Meerdaal forest on a fairly large scale. Before this, between 1740 and 1770, the sandy areas got already planted with coniferous trees. The areas chosen for the plantation of beech trees depends on the soil type as well. These beech trees got planted on the areas with the least productive coppice with standards plots. On the more productive patches, coppice with standards with oak remained the chosen management strategy up until the twentieth century.

From the twentieth century onwards more detailed information about the forest composition can be found (Antoine, 1913; Blondeau, 1910; Bossu, 1911a, 1911b). One such detailed source of information is a report from a forestry excursion in 1937 (Brichet, 1938). According to this source the standards trees were predominantly oak trees (*Quercus robur and Quercues patraea*), supplemented with beech (*Fagus sylvatica*), ash (*Fraxinus excelsior*), poplar (*Populus canescens*), and some other tree species. Hazel (*Corylus avellana*) was the most dominant species in the coppice layer, supplemented with European common hornbeam (*Carpinus betulus*), oak (*Fagus sp.*), sycamore (*Acer pseudoplatanus*), and sweet chestnut (*Castanea sativa*). The standards were planted at a relative high density, making the coppice wood less productive than few generations ago. However, due to the shade tolerance of hazel most of the coppice was still very vital (De Keersmaeker et al., 2009).

The last real coppice harvests were done in the early 1950's. In the management plan of 1963 only 6 ha is still marked as coppice with standards. From then on, the foresters resolutely opted for group clear felling with openings of 10-20 ares. This led to the true transformation from coppice with standards to high forest (De Keersmaeker et al., 2009). In this high forest, patch clearcutting was the practice chosen for wood harvest. Originally, these patches were quite small (10 are). After cutting, these patches were replanted with mostly beech, native oak species and in lesser numbers with ash trees. The next felling was connected to the existing groups, resulting in a systematic increase of felt area. From the 1970s onwards, the patches were made larger (20-30 ares). During the last 2 decennia of clearcutting these groups were made even larger (over 50 ares). In these last decades, also no beech trees got planted anymore in the areas dominated with oak trees. The stands were also regularly thinned over the last decades (De Keersmaeker et al., 2009; Vandekerkhove et al., 2021).

Since 1995, Everzwijnbad and Pruikenmakers are classified as forest reserve. They form a part of the larger “bosreservaat Meerdaalwoud” (Baeté et al., 2004; Baeté et al., 2007). The last thinning took place 2-5 years before the establishment of these forest reserves (Vandekerkhove et al., 2021). Later, in 2000 the forest reserves gained the statute of integral forest reserve. Since then, a zero-management strategy is applied. However, some introductory management was still carried out in the first years, especially in Pruikenmakers. At forest reserve Everzwijnbad there was only very limited need for introductory management.

Introductory management at Everzwijnbad included further reduction of the public accessibility, the removal of northern red oak (*Quercus rubra*) and the control of against black cherry (*Prunus* *serotina*). Introductory management at Pruikenmakers was somewhat more elaborate. During the period 1998-2002 there were control actions against *Prunus serotina* and *Quercus rubra*. In the fringe zones, of more or less 30 m, northern red oak got cleared. More central in the reserves the chosen control method was ringbarking. However, since the low number of these exotic trees, these actions were only limited. In the sandy zone in the southwest of the forest reserve most interventions were needed. Here, in 2008-2009 some remaining northern red oaks were cleared. In 2000, a small patch with Corsican pine (*Pinus nigra*) was cleared. In the larger pine forest part, located around the sand quarry, a strong thinning was done in order to promote other native tree species. On several locations it was also planned to give room to rare native tree species. The plan was to cut obstructive surrounding trees within a radius of 15 meter. However, this was eventually only carried out for some wild apple trees (European crab apple or *Malus sylvestris*). Also, some trees were cut that could form a potential danger for pedestrians. Since 2002 most walking roads in the forest reserve are closed to the public. Only the Eleonoradreef, which runs in a north-south direction trough the reserve, is still freely accessible. Also, some Douglas fir (*Pseudotsuga menziesii*) were cleared in the western part of Pruikenmakers near the "verdroogde vijver" site. According to the management plan of 1998 (Meuleman, 1998) the goal was to rewet this area as well, this has not been realized yet. The plan is that eventually the Eleonoradreef will gradually disappear and become an integral part of the forest reserve Pruikenmakers. Also, most of the Walendreef (north border of the reserve) will be removed by felling of the trees, followed by inclusion in the forest reserve (De Keersmaeker et al., 2009).

1.8 Vegetation

Following the EEA (2007) classification, the forest reserves are classified as Sub-Atlantic mesophytic pedunculate oak-hornbeam forests situated on fertile loess deposit soils (Vandekerkhove et al., 2021). Well-developed phytosociological communities characterize both forest reserves. Many characteristic ground vegetation species typical for ancient woodlands on fertile loess soils are present. The two forest reserves are generally categorized as Sub-Atlantic forms of *Stellario-Carpinetum* and *Milo-Fagetum* (Noirfalise, 1984; Vandekerkhove et al., 2021). However, pronounced presence of micro-gradient differences between mineral-rich and mineral-poor soil types, variations in moisture and mineral balance as a result of soil compaction, and effects of tree species make a simple, general categorization difficult (De Keersmaeker et al., 2005a).

1.8.1 Everzwijnbad

1.8.1.1 General description

Everzwijnbad is characterized as a high forest with native oak species (*Quercus robur* and *Quercus petraea*) with an admixture of *Acer pseudoplatanus*, *Fraxinus excelsior*, *Prunus avium*, *Populus canescens, Larix sp*., *Betula pendula* and *Carpinus betulus*. Prior to 2000, also *Quercus rubra* was commonly present. As mentioned above, ringbarking of these trees led to the reduction of this exotic species. Furthermore, some strips of *Fagus sylvatica* high forest are present. Dominant tree species in the shrub layer are *Carpinus betulus* and *Corylus avellana*. Remarkably, also *Ilex aquifolium* is quite present in this shrub layer. The herb layer mainly consists of species that are shade and acid tolerant (e.g., *Milium effusum* and *Oxalis acetosella*). However, locally acid avoiding species can occur (e.g., *Melica uniflora* and *Paris quadrifolia*). The reserve is a good representative of *Millo-Fagetum*, *Fago-Quercetum* (on the poorest/most acidic soils) and *Stellario-Carpinetum* (on the richest/least acidic soils) (Baeté et al., 2004; Meuleman, 2006; Vandekerkhove et al., 2021).

1.8.1.2 Vegetation types

In 1954, 70 vegetation relevés were carried out in the Meerdaal forest (Déthioux, 1955). The collected data was used to create a vegetation map for the Meerdaal forest, which is a part of the Vegetation map of Belgium ("Vegetatiekaart van België (1959)": map sheet Hamme-Mille 103E (Déthioux, 1959)). Later in 2002-2003 a new vegetation map (figure 19 and 22) was created. A similar classification as the one by Déthioux (1959) was used. This map is based on the vegetation samples of Bauwens (2001) and vegetation data collected for the management plan of the Meerdaal forest (Roelandt, 2004). Figure 19 gives a detail of this map for Everzwijnbad. The following vegetation types are present:

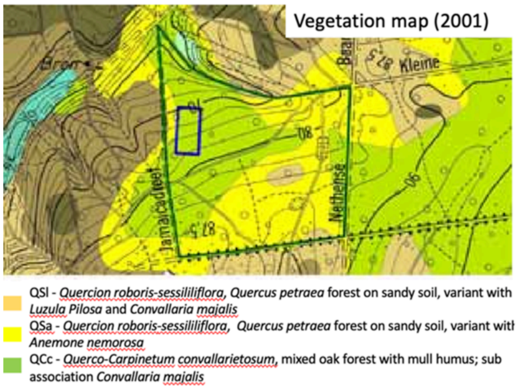
- Green: Oak-Hornbeam forest with mull humus; sub-association *Convallaria majalis* (QCc)
- Yellow: Oak-Beech forest; sub-association *Anemone nemorosa* (QSa)
- Beige: Oak-Beech forest; sub-association *Luzula Pilosa* and *Convallaria majalis* (QSl)

Typical tree species of the Oak-Hornbeam forest (QC) vegetation type are: *Quercus robur, Acer pseudoplatanus, Fagus sylvatica, Corylus avellana, Fraxinus excelsior, Carpinus betulus, Populus canescens, Prunus avium, Tilia cordata* and *Ulmus minor*. Typical herbaceous species are: *Anemone nemorosa, Millium effusum, Oxalis acetosella, Athyrium felix-femina, Lamium galeobdolon, Polygonatum multiflorum, Hedera helix, Convallaria majalis, Melica uniflora, Adoxa moschatellina, Paris quadrifolia,* and *Veronica montana* (Meuleman 2006).

Typical tree species of the Oak-Beech forest (QS) vegetation type are: *Fagus sylvatica, Pinus sylvestris, Castanea sativa, Quercus rubra, Betula pendula, Quercus robur* and *Acer pseudoplatanus.* Typical herbaceous species are: *Carex pilulifera, Pteridium aquilinum, Convallaria majalis, Dryopteris filix-mas, Maianthemum bifolium, Teucrium scorodonia, Hypericum pulchrum, Rubus idaeus, Anemone nemorosa* and natural rejuvenation of *Quercus rubra* and *Fagus sylvatica* (Meuleman 2006).

According to Déthioux (1959), the QCc vegetation type can be seen as the intermediate between *Quercetum atlanticum* (Atlantic mixed oak forest) and the *Querceto-carpinetum* (Center-European oak-hornbeam forest). The classification deviates from the *Quercetum atlanticum* due to the absence of *Hyacinthoides non-scripta*. The presence of acid tolerant species like *Holcus molis*, *Luzula pilosa*, *Lonicera periclymenum*, *Oxalis acetosella*, *Dryopteris dilatata* and *Convallaria majalis* determines the classification into the sub association *"Convallaria majalis"*. Typical for the subvariant QSa are species with higher soil demands like *Anemone nemorosa*, *Oxalis acetosella*, *Polygonatum multiflorum* and *Hedera helix*. QSa can be seen as a transition from mull humus (QCc) to a rougher moder type of humus. This QSa zone in the forest reserve resembles greatly with the younger beech and oak stands in the southeastern part of the reserve. A small area is classified as QSl, a variant of the Oak-Beech forest with *Luzula pilosa* and *Convallaria majalis* (De Keersmaeker et al., 2005a; Déthioux, 1959).

Figure 20 gives the second version of the Biological Valuation map (Guelinckx et al., 2002) for forest reserve Everzwijnbad. According to this map the forest reserve is located in a biological very valuable area. This map classifies the forest reserve as: (1) qa + fa, a complex of Oak-Hornbeam forest (*Stellario-Carpinetum*) and Beech forest with vernal flora (absence of *Hyaconthoides non-scripta*) (*Milo-Fagetum);* (2) fs + qs, a complex of acidic Beech forest and acidic Oak forest (*Fago-Quercetum*); (3) fs, an acidic Beech forest (*Fago-Quercetum*); and (4) qs, an acidic Oak forest (*Fago-Quercetum*).



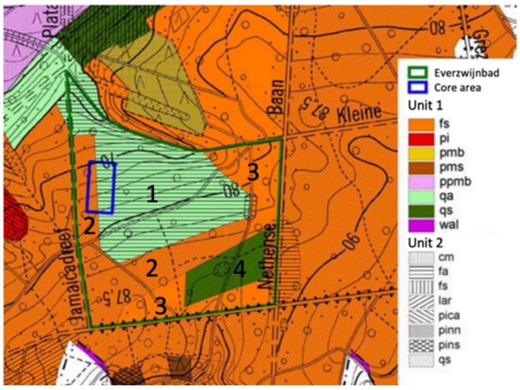


Figure 19: Vegetation mapping in Everzwijnbad (Roelandt, 2004)

Figure 20: Bioligical valuation map of Everzwijnbad (version 2) (Guelinckx et al., 2002)

When comparing these maps (figure 19 and 10), we can see that both maps divide the area in a "richer" (respectively QCc and qa + fa) and "poorer" (respectively QSa + QSl and qs + fs) part.

A basic inventory of the forest reserves of the Meerdaal forest was done in 1997 (Van Mechelen et al.). A Twinspan analysis of the collected data led to classification of Everzwijnbad in 9 more or less homogenous parts (figure 21). The herb layer type *Millium effusum-Oxalis acetosella* is the most dominant. This type belongs to the "richer" vegetation type in this forest reserve. The presence of this type is positively correlated with the presence of native oaks and in lesser abundance *Acer pseudoplatanus*, in the tree layer. The "poorer" herbaceous understory vegetation types *Dryopteris-Fagus*, *Convollaria majalis-Fagus* and *Pteridium aquilinum-Fagus* are present in the areas dominated by beech trees (De Keersmaeker et al., 2005a).

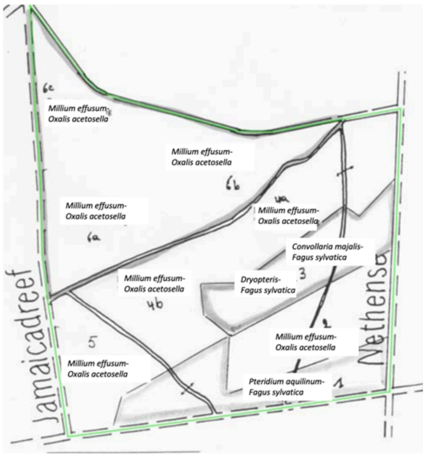


Figure 21: Herb layer types in 1996 (Van Mechelen et al., 1997)

De Keersmaeker et al. (2005a) found in their monitoring report, using the same plots as in this study (see chapter 2.1 Sampling design), the presence of 51 plant species in the understory. A large part of these are ancient woodland plants, indicating prolonged presence of forest. The most frequently observed species in descending order are: *Dryopteris dilatate*, *Milium effusum*, *Anemone nemorosa*, *Athyrium filix-femina*, *Rubus sp.* and *Oxalis acetosella*. Species with the highest cover are (empty plots not included): *Oxalis acetosella*, *Holcus lanatus*, *Athyrium filix-femina* and *Lamium galeobdolon*. Species found that are not very common and rare in Flanders are: *Lysimachia nemorum*, *Carex pallescens*, *Melica uniflora*, *Veronica montana*, *Potentilla sterilis* and *Festuca gigantea*. They conclude that the vegetation in Everzwijnbad is quite varied, with a large part of ancient woodland species. It varies from a *Stellario-Carpinetum* on the richest/least acidic soils, to a *Fago-Quercetum* on the poorest/most acidic soils with a sandy substrate. The *Millo-Fagetum* has an intermediate position and covers the largest part of the forest reserve (De Keersmaeker et al., 2005a).

1.8.2 Pruikenmakers

1.8.2.1 General discription

Forest reserve Pruikenmakers mainly consists out of a high oak forest dating from 1790-1840 with an admixture of *Fagus sylvatica*, *Fraxinus excelsior*, *Quercus rubra*, *Betula sp.*, *Acer pseudoplatanus* and *Populus canescens*. Parts dominated by *Fagus sylvatica* are also present. Groups of *Quercus robur*, *Quercus petraea* and *Fagus sylvatica* were planted since 1955 for forest rejuvenation. Around 1950, a stand of coniferous trees was planted on the highest, sandy part. Pruikenmakers is also characterized by numerous secondary native tree species: e.g., *Tilia cordata, Malus sylvestris*, *Mespilus germanica*, *Crataegus sp.* and *Ulmus* *sp*. The reserve is a good representative of *Millo-Fagetum* and *Stellario-Carpinetum* forest (Meuleman, 2006)

1.8.2.2 Vegetation types

A said above, in 1954 70 vegetation relevés were caried out in the Meerdaal forest (Déthioux, 1955). The collected data was used to create a vegetation map for the Meerdaal forest, which is a part of the Vegetation map of Belgium ("Vegetatiekaart van België (1959)": map sheet Hamme-Mille 103E) (Déthioux, 1959). Based on these older vegetation types of Pruikenmakers we can state that there is a strong link between soil type and soil richness and the present vegetation type. The loamy soils were categorized as Oak-Hornbeam forest with mull humus: *Querco-Carpinetum* (QC) and the variant *Querco-Carpinetum convallarietosum* (QCc). The subvariant QCc was the most dominant one. Smaller strips in the northeast and the west were categorized as the variant with *Stachys sylvatica*, indicating a somewhat richer soil. The sandy, poorer parts in the southwest were categorized as coniferous plantations. In these plantations vegetations characterized by *Calluna vulgaris* with *Vaccium myrtillus* and *Calluna vulgaris* with *Genista angelica* were present. More central a *Quercus petraea* forest planted with coniferous trees and an Oak-Beech forest with *Anemone nemorosa* (QSa) was present.

Figure 22 gives a detail for Pruikenmakers from the management plan of 2006 (Meuleman). This map is based on the vegetation map of 2002. As mentioned above, they used a similar classification as the one by Déthioux (1959). The classification in vegetation types is based on the vegetation samples of Bauwens (2001) and vegetation data collected for the management plan of the Meerdaal forest (Roelandt, 2004). The following vegetation types are present:

- Light green: Oak-Hornbeam forest with mull humus; sub-association *Convallaria majalis* (QCc)
- Green: Typical Oak-Hornbeam forest (QC)
- Dark green: Oak-Hornbeam forest (QC), variant *Stachys sylvatica* (somewhat richer soils)
- Orange: Oak-Beech forest (QS)
- Red: Oak-Beech forest; sub-association *Anemone nemorosa* (QSa)
- Beige: Oak-Birch forest (QB)

Typical tree species of the Oak-Hornbeam forest (QC) vegetation type are: *Quercus robur, Acer pseudoplatanus, Fagus sylvatica, Corylus avellana, Fraxinus excelsior, Carpinus betulus, Populus canescens, Prunus avium, Tilia cordata* and *Ulmus minor*. Typical herbaceous species are: *Anemone nemorosa, Millium effusum, Oxalis acetosella, Athyrium felix-femina, Lamium galeobdolon, Polygonatum multiflorum, Hedera helix, Convallaria majalis, Melica uniflora, Adoxa moschatellina, Paris quadrifolia,* and *Veronica montana* (Meuleman, 2006)

Typical tree species of the Oak-Beech forest (QS) vegetation type are: *Fagus sylvatica, Pinus sylvestris, Castanea sativa, Quercus rubra, Betula pendula, Quercus robur* and *Acer pseudoplatanus.* Typical herbaceous species are: *Carex pilulifera, Pteridium aquilinum, Convallaria majalis, Dryopteris filix-mas, Maianthemum bifolium, Teucrium scorodonia, Hypericum pulchrum, Rubus idaeus, Anemone nemorosa* and natural rejuvenation of *Quercus rubra* and *Fagus sylvatica* (Meuleman, 2006).

Typical tree species of the Oak-Birch forest (QB) vegetation type are: *Pinus sylvestris, Betula pendula, Fagus sylvatica, Quercus rubra, Quercus robur, Castanea sativa, Sorbus aucuparia* and *Prunus serotina*. Typical herbaceous species are: *Mollinia caerulea, Deschampsia flexuosa, Vaccinium myrtillus, Calluna vulgaris, Dryopteris dilatate* and *Lonicera periclymenum* (Meuleman, 2006).

Figure 23 gives the Biological Valuation map (Guelinckx et al., 2002) for forest reserve Pruikenmakers. According to this map the forest reserve Pruikenmakers is a biological very valuable area. According to this map Pruikenmakers can be classified as:

- qa: Oak-Hornbeam forest (*Stellario-Carpinetum*)
- qs: acidic Oak forest (*Fago-Quercetum*)
- cm: degraded heathland with dominance of *Molinia caerulea*
- cmb: *Mollinia caerulea* dominated heathland with shrub or tree growth
- cp: degraded heathland with dominance of *Pteridium aquilinum*
- pmb: coniferous plantation with undergrowth of shrub and trees
- pmh: coniferous plantation with undergrowth of grasses
- ppms: *Pinus silvestris* plantation with low undergrowth (Brambles, brooms, heather and ferns)
- ppmh: *Pinus silvestris* plantation with undergrowth of grasses

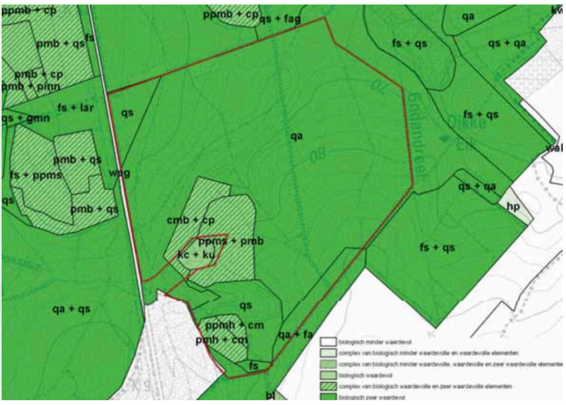


Figure 22: Vegetation mapping in Pruikenmakers (Meuleman, 2006), based on Roelandt (2004)

Figure 23: Bioligical valuation map of Everzwijnbad (version 2) (Guelinckx et al., 2002)

De Keersmaeker et al (2009) created a detailed vegetation map of the herbaceous understory (Figure 24). This classification of the herbaceous understory types resembles largely the natural topography, light conditions and former land use.

Figure 24: Vegetation facies mapping in Pruikenmakers (De Keersmaeker et al., 2009)

The largest part (figure 24, Type 1) was categorized sensu Cornelis et al. (2009) as Ash-Oak forest with *Millium effusum* and *Oxalis acetosella*. *Anemone nemorosa, Stellaria holostea, Lamium galeobdolon* and *Athyrium filix-femina* are characteristic species of this vegetation type. The valley running through the reserve is characterized by a somewhat richer variant of the previous with *Dryopteris carthusiana* as characteristic species (Type 4).

On the higher, sandy area they found a previously logged area with *Mollinia caerulea* and shrub or tree growth (Type 14). In the northwest and surrounding the previous described logged area, zones characterized by *Pteridium aquilinum* are present (Type 12). Cornelis et al. (2009) describe this vegetation type as Oak-Beech forest with *Pteridium aquilinum.* In the south of the reserve there is a light-rich zone with dominance of *Pteridium aquilinum* (Type 13). On the sandy area, locally also *Dryopteris dilatata* and brambles can have an important role (Type 11).

The presence of calcareous loam at the gully incisions in the south leads to the presence of typical species like *Primula elatior, Paris quadrifolia* and *Arum maculatum* (Type 6). Cornelis et al. (2009) describe this vegetation type as Ash-Alder forest with *Arum maculatum*.

Vinca minor is dominant in a fairly large zone in the northwest (Type 7 and 8). This species is also dominant on a small area along the Eleonoradreef (Type 7). The dominance of *Vinca minor* is often an indication of somewhat richer loamy soils, for example due to past agricultural practices.

The blue polygon indicates a former pond. This pond was dried up and planted with *Pseudotsuga menziessi* in the past. After the designation of Pruikenmakers as forest reserve this *Pseudotsuga menziessi* stand was logged and left behind. The management goal is to rewet this area (Meuleman, 1998).

De Keersmaeker et al. (2009) found in their monitoring report, using the same plots as in this study (see chapter 2.1 Sampling design), the presence of 64 plant species in the understory. Many of them can be categorized as ancient woodland species, indicating prolonged presence of forest. The most frequently observed species in descending order are: *Rubus sp.*, *Dryopteris carthusiana*, *Anemone nemorosa*, Dryopteris dilatata, *Athyrium filix-femina*, *Millium effusum* and *Holcus lanatus*. Species with the highest cover are (empty plots not included): *Anemone nemorosa*, *Ranunculus ficaria*, *Molinia caerulea* and *Deschampsia flexuosa*. They conclude that the forest reserve Pruikenmakers has a high species diversity. This diversity is linked with the habitat heterogeneity of the reserve. In general, loamy soils are dominant. But in the south, locally calcareous soils are present along the gully incisions. Leading to the presence of typical species like *Primula elatior, Paris quadrifolia, Rubus caesius* and *Chrysosplenium oppostifolium*. More northwards locally sandy soils are present with typical species like *Calluna vulgaris* and *Vaccinium myrtillus*.

1.9 Management goals and current management (2006-2025)

As said above, since 1995 both reserves are classified as forest reserves. Last thinnings took place 2-5 year prior to this. Since 2000, the reserves got the statute of integral forest reserves. Resulting in a zero-management strategy (Baeté et al., 2004; Baeté et al., 2007; Vandekerkhove et al., 2021).

According to the management plan for 2006-2025 from Meuleman (2006), the goal for the Meerdaal forest in its whole is that it can grow without any problems into a textbook example of a multifunctional forest located in a region with one of the highest human populations in Western-Europe. Ecologically this means a restoration of the *Stellario-Carpinetum* forest and the linkages with the Dyle valley, the Heverleebos and the European badger population in Walloon Brabant. Economically this indicates a shift in production function towards solely quality wood production of mainly native common oak and secondary tree species, accompanied by a decrease in beech and exotic coniferous trees. Also, restoration of coppice wood and rejuvenation of common oak and secondary tree species will gain considerable attention. The big, old oaks, which are crucial for many organisms, will be saved from expanding beech trees. An important increase in the amount of open spaces can be expected. An important point of attention here will be the start of grazing management, for example at the former military domain and surrounding pastures. One of the goals is to both increase the ecological value of the Meerdaal forest, while also providing space for recreants and tourism (Meuleman, 2006).

The forest reserves play an important role in these general goals for the forest complex Meerdaal forest. Aims for the forest reserves themselves, are: improvement of the natural fauna and flora, improvement of the native tree species, improvement of the natural rejuvenation, improvement of different age classes and forest structure and improvement of ecological balance. Pruikenmakers is characterized by the presence of many different native tree species, like *Tilia cordata, Malus sylvestris*, *Mespilus germanica*, *Crataegus sp.* and *Ulmus sp.*. This can be of importance for future reintroduction in areas where these species have disappeared (Meuleman, 2006).

No further management actions in the reserves are coupled with the current management goals. A possible danger of this zero-management strategy at Pruikenmakers is that the rare and valuable tree species like *Tilia cordata, Malus sylvestris* and *Mespilus germanica* will be supressed, resulting in a decrease in fruit production. These secondary trees species will only be represented well in a very vast forest with all stages of succession (Meuleman, 2006).

The previous centuries of forest management and associated disturbances in these forest reserves have altered these forests in both structural features and species composition compared to old growth forest. Therefore, another danger of introducing non-intervention management in formerly managed forest is a reduction in the share and frequency of canopy and soil disturbances due to wood harvest (Heinrichs & Schmidt, 2017; Vandekerkhove et al., 2021). This lower disturbance frequency may lead to a continued closed canopy and continued deep shading during their transition phase towards old forest where natural disturbances reappear (Scherzinger, 1996; Vandekerkhove et al., 2021). Therefore, according to the intermediate disturbance theory (Connell, 1978), detrimental effects on species richness are possible. Former management regimes have led to increased soil disturbances and sun-exposed conditions. These past conditions, especially for stands with long management traditions such as coppicing, may have developed species rich communities including heliophilous species and thermophilous species (Vandekerkhove et al., 2021).

Vandekerkhove et al. (2021) recently focused on the effects of the introduction of a non-intervention strategy in previously managed forests on the ground vegetation development in four strict management reserves (including Everzwijnbad and Pruikenmakers) on the plateau of Brabant. They investigated vegetation changes after the cessation of forest management in the context of continued deep shade during the transition period towards old growth. Analyses were done on two repeated surveys with an interval of 10 years in these recently non-managed forests.

They found that an overall loss in species richness has occurred at all sites. They also detected a trend towards the homogenization of the vegetation due to a reduction in disturbance related and anthropogenic related species. However, reduced disturbance and increased shading did not result in negative effects for all species. The species richness of vernal geophytes and typical shade-tolerant species remained the same, while at the same time there cover significantly increased. Vandekerkhove et al. (2021) state in their conclusion that this trend towards a mesic forest is often seen as a loss of natural value and diversity (Heinrichs & Schmidt, 2017; Hédl et al., 2010; Van Calster et al., 2007), but it can also be considered as a natural restoration and succession towards more natural and authentic vegetation where species richness of vascular plants is generally lower. In these systems light-demanding species are rare and ephemeral, which is harmonious with natural disturbance regimes. In line with this second context, high plant species diversity indicates management related disturbances, instead of a forest conservation status (Boch et al., 2013; Burrascano et al., 2017; Lelli et al., 2019; Vandekerkhove et al., 2021).

When we look at the wider context of the forest complex Meerdaalwoud, these losses are only happening at a local scale. Also, often these losses are only temporary. After the transition phase towards old growth, natural disturbance will again increase (Scherzinger, 1996). Also, many of these lost species are adapted to the ephemeral and infrequent disturbance events that occur in unmanaged forests. Often, they can quickly reestablish after disturbance due to their good dispersal abilities and long-lasting seed bank. Meanwhile these lost species also may subsist in the neighboring managed forests. Forest reserves Everzwijnbad and Pruikenmakers are embedded in a larger forest complex that is mainly managed through small-scaled harvest interventions. Therefore, in regions with an extensive history of active management, a combined approach will give the best assurance of development and overall conservation of forest biodiversity (Bollmann & Braunisch, 2013; Doerfler et al., 2018; Vandekerkhove et al., 2021). Risk of loss of certain species in these forest reserves should not be a plea to exclude the installation of new non-intervention reserves (Vandekerkhove et al., 2021).

2 Data samping

2.1 Sampling design

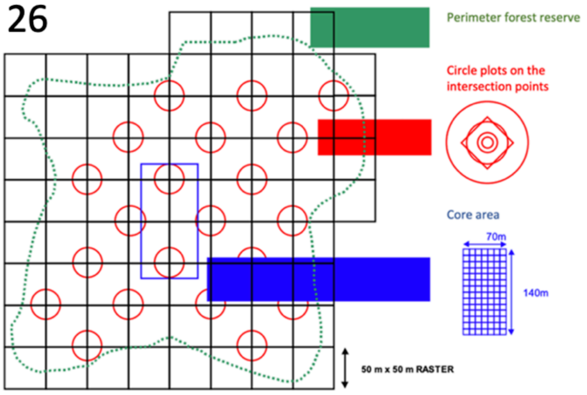
In 2005 De Keersmaeker et al. created a standard methodology for assessing and monitoring the integral forest reserves in Flanders. The used sampling design in this study is based on this monitoring program for integral forest reserves (De Keersmaeker et al., 2005b). Therefore, the methods used in this study are similar and compatible with the Flemish Forest Inventory and the sampling methods used for management plans. Our study area, Pruikenmakers and Everzwijnbad, are a part of the integral forest reserves in Flanders. And thus, a sampling design has already been created and used in previous research (e.g, (De Keersmaeker et al., 2005a; De Keersmaeker et al., 2009; De Keersmaeker et al., 2005b). Both forest reserves are divided in smaller units using a rectangular grid. This grid was then used to assign circle plots in each forest reserve. The goal of this arrangement using a grid is to give a global and representative image of the entire study areas. The center of each plot has been assigned a permanent number. 101-148 for Everzwijnbad and 901-966 for Pruikenmakers. These centers have been marked with a permanent feno marker (figure 25) (De Keersmaeker et al., 2005b).

Figure 25: Example of a numbere feno marker used to indicate the center of each plot. Picture: Hendrik Willems

Figure 26 gives a schematic overview of the sampling design. A grid of 50 x 50m has been chosen for the division of the study area. In a systematic way the centers of the circle plots were assigned to half of the intersection points of the grid. On each of these central points four nested circular plots were created. The radius of these circle plots are adapted to the dimensions of the trees and shrubs in these plots (De Keersmaeker et al., 2005a; De Keersmaeker et al., 2005b). The core areas shown on the figure are not applicable in this thesis.

These nested circular plots were used for dendrometric monitoring in the past. These measurements were made available for this study as well (De Keersmaeker et al., 2005a; De Keersmaeker et al., 2009). The largest of the nested circular plots (r = 18 m) were used to measure and position all living trees with a DBH of 40 cm or higher. All dead wood with a diameter of 5 cm or more was measured and positioned as well in these plots. The second largest circles (r = 9 m) were used to measure and position all trees and shrubs with a DBH between 5 and 40 cm. All species names, diameters, and heights of these sampled trees in these two biggest circular plots were collected. The nested circular plots with r = 4.5 m and r = 2.25 m were used to measure the rejuvenation of trees and shrubs with a DBH < 5 cm. These were counted in height classes. The data collected in these two smallest circles were not positioned geographically (De Keersmaeker et al., 2005a)

At the centers of each plot a vegetation relevé was performed. For this 16 by 16 m square plots are used (figure 27). The diagonal axes of these squares were oriented north-south and east-west (De Keersmaeker, Baeté, et al., 2005). These square plots were also used in our study for the assessment of the vegetation and the impact of wild boar.



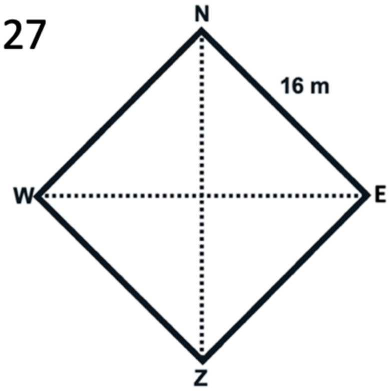
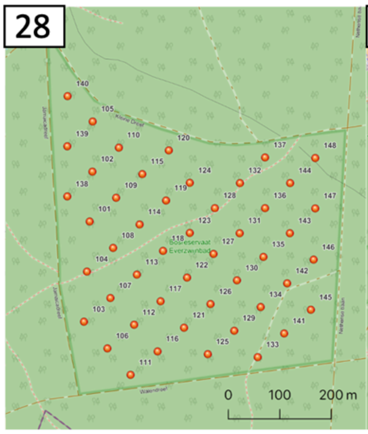


Figure 26: Schematic overview of the monitoring layout with grid-based circle plots, the core area (Blue) is not applicable in this case. Center circle plots were used to create square plots (De Keersmaeker, Van de Kerckhove, et al., 2005)

Figure 27: Example of the 16 by 16m square plot with N-Z E-W orientation

For Everzwijnbad the standard grid has been set out parallel with the Nethense Baan, resulting in a total of 48 square plots (figure 28) (De Keersmaeker et al., 2005b). For Pruikenmakers the standard grid was set out parallel with the Eleonaredreef, which runs as a central axis through the forest reserve (figure 29). Close to the paths and roads a perimeter was respected in which no circle plots were placed, this resulted in a total of 66 square plots for forest reserve Pruikenmakers (De Keersmaeker et al., 2009).



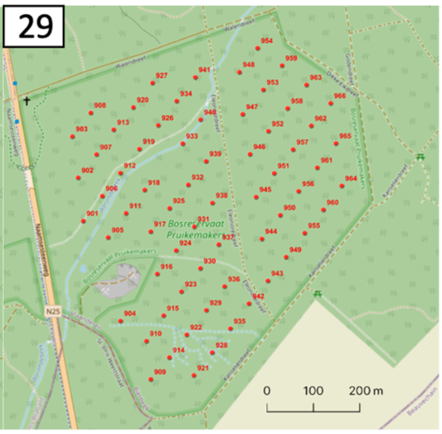


Figure 28: Location and numbering of the 48 circle plots in forest reserve Everzwijnbad

Figure 29: Location and numbering of the 66 circle plots in forest reserve Pruikenmakers

2.2 Vegetation and rooting sampling

Each permanent square plot in Everzwijnbad and Pruikenmakers was surveyed during August-September 2020. The plots were surveyed for wild boar rooting intensity, occurrence of plant species, percentage cover of each plant species and total percentage plant cover per plot. Also, extra information like the occurrence of intensive rooting signs with particular plant species distance to roads or trails and other conspicuous conditions were noted down. Two vegetation surveys had already been carried out by the staff of the forest ecology research team of INBO in these forest reserves. They did this in 2003-2013 and 2005-2015 for respectively Everzwijnbad and Pruikenmakers. The vegetation relevés carried out by the research team of INBO were done in April and June. Both records were later combined into one result taking into account the record with the highest cover. In these vegetation relevés also overall coverage of shrub and tree layer were registered (Vandekerkhove et al., 2021). Other support data like dendrometric and soil variables were also collected made available by the research team of INBO. Soil variables were only measured during the first survey (2003-2005). Dendrometric variables were collected in winter for the first two surveys (2003-2005 and 2013-2015).

As said before, the return of wild boar for Flanders occurred only after 2006, so vegetation data from before and after the arrival is available. The data from 2003 and 2005, or survey 1, is a snapshot from a situation without wild boar. The data gathered in 2013 and 2015, or survey 2, represent a time where wild boar had already returned in the Meerdaal forest but were still at low population densities. And finally, the data gathered in 2000, or survey 3, is a snapshot from a situation where wild boar populations densities are increasing. Other support data like dendrometric varaibles, soil variables and coordinates of each plot were also made available by the research team of INBO.

2.2.1 Rooting data collection

We used a similar rooting sampling design as proposed by Burrascano et al. (2015). Rooting intensity was measured through counts of single rooting signs in each plot. Each sign of an approximately 15 cm-wide space of disturbed ground was counted as one individual rooting sign. Wider signs were noted as multiples of one single sign, for example 45 cm-wide signs equals 3 rooting signs. Only clear and fresh signs were counted. These were defined and delineated as follows: bare soil, not covered by fallen leaves or vegetation, and conclusive with sign of rooting by wild boar. Not considered were unclear signs (inconclusively to be assigned to wild boar), or old traces, no longer consisting of bare soil but covered by fallen leaves or living plants (indicating that they are at least from previous year). This method of rooting data collection presents a snapshot measure of wild boar disturbance, since detailed long-term data on wild boar disturbance cannot be derived from it (Burrascano et al., 2015). All rooting signs in each 16 by 16m plot were counted. For this the square plot was divided in strips of about 3 meters. Each of these strips were surveyed one by one to count the total number of rooting signs per plot. In this way plots with contrasting levels of rooting intensity could be derived. This can later be used to analyze the response of understory vegetation to different levels of rooting/disturbance intensity.

2.2.2 Understory vegetation sampling

Each 16 by 16m square plot was divided in strips of approximately 3 meters, the same as was done for the rooting intensity sampling. Within each strip we registered the occurrence of each vascular plant species in the understory vegetation. The data gathered of each strip of the same plot was combined into the actual data of the square plot. Also, the percentage cover of each plant species was estimated per plot. Finally, the total plant cover per plot was estimated. All plants in the understory as well as small trees up to 1 meter were surveyed. If the plots were dominated by larger tree rejuvenation (>1m) this was recorded as a comment for that plot.

2.2.3 Pseudoreplication

It is important to know that the plots examined in Everzwijnbad or Pruikenmakers cannot be seen as true independent replicates. These forest reserves are of course not identical and examined plots in each forest reserve can therefore be seen as subsamples rather than as independent samples. This is an important limitation in this study. Forest reserve was added as an extra random factor to account for repeated sub samples in the data analysis where possible (Millar & Anderson, 2004). And in some cases, analysis was done on subsets of the dataset containing either only data from Everzwijnbad or Pruikenmakers.

3 Data analysis

3.1 Preparatory work

All measured and provided data was imported and managed in Microsoft Excel®. Data calculation and analysis was performed in RStudio version 1.4 with R version 4.04 (R Core Team, 2021). A first step was to compile a dataset of the data collected during this thesis and the data from previous surveys provided by INBO. Several plots where not integrated in the data from the first two surveys. Therefore, these plots (112, 130, 904, 909, 911, 914, 915, 916, 917, 923, 932, 946 and 957) were excluded from the dataset. This resulted in a total of 101 plots, 46 in Everzwijnbad and 55 in Pruikenmakers. Since vegetation relevés in 2020 were only done in summer, also all vernal flora were excluded from this dataset. Unless noted otherwise analysis were dan on this final dataset.

Using this final dataset, several extra variables were calculated. Table 1 gives a summary of all available variables. Each of these variables were measured or calculated at individual plot level. Soil variables were only measured during the first survey by the research team of INBO. Dendrometric variables were only measured during the first and the second survey by the research team of INBO. Finally, rooting variables were only measured during the third survey. Variables were divided in understory plant related variables, soil variables, dendrometric variables and wild rooting intensity variables. Variables with an asterisk were measured directly, other variables are derived from these directly measured variables. Number of rooting sings was also transformed to a categorical variable for some analyses. Based on the quantiles 4 groups were constructed: None/Very low rooting (n = 25, 0-6 signs), Low rooting (n = 24, 6-11 signs), Moderate rooting (n = 26, 12-25 signs) and High rooting intensity (n = 26, 26-138 signs).

Table 1: Overview all available measured and derived variables

Plant variables		Soil variables	Dendrometric variables		Rooting variables
Abundance data of all plant species *	Number anciet woodland species (AWS)	Sand fraction *	% Shrub *	BA Fagus *	Number of rooting tracks *
Coverage understory (%) *	Relative number AWS (#AWS/#species)	Loam fraction *	% Tree *	BA Quercus *	Categorical rooting classes
Species richness	Number stress tolerant species	Clay fraction *	Shade casting index	BA Populus *	
True Shannon diversity	Number light demanding species	pH CaCl2 value *	Litter quality	BA Other *	
Inverse Simpson diversity	Number competitor species	Kjeldahl N value *	% Cover shrub + tree	% Fagus BA	
Eveness	Cover stress tolerant	OM Gloeiverlies *	Above ground biomass *	% Quercus BA	
Cover Phanerophytes	Cover light demanding	Plant available Phosphor *	Lying dead wood *	% Populus BA	
Cover Geophytes	Cover competitors	CEC BaCl2 *	Standing dead wood *	% Other BA	
Cover Hemicryptophytes	Cover Ellenberg values plot (L, F, R and N)				
Cover Therophytes	Cover C, S and R value plot				
Cover Chamaephytes					

The collected plot data of the understory plant species were used to calculate all other plant related variables. Surveys were compared to examine which species disappeared through the years and total species richness of each survey was determined. Average characteristic cover (excluding plots with species absence) and frequencies were calculated for every species. This was done per survey and for the combination of survey and rooting class. Hill numbers were used as the family of diversity measures to calculate species richness, True Shannon diversity (exponential Shannon diversity), true Simpson diversity (inverse Gini-Simpson) and evenness (Hill, 1973) using the “hillR” package (Li, 2018). A set of characteristics and indicator functional trait values were assigned to each species found in the herb layer. Species lifeforms were determined according to Raunkiær (1934). Ancient woodland species (AWS) were determined according to Hermy et. al. (1999). Ellenberg indicator values for each species were calculated as the mean Ellenberg between the classification according to Ellenberg et al. (2001) and Hill et al (1999). CSR-strategies were derived from Grime (1979) and were expressed in functional signatures scores using Hunt et al. (2004). Plant species with Ellenberg indicator value L of 6 or higher were classified as light demanding species. An indicator value as stress tolerant and competitor species was derived based on their CSR value according to Hunt et al. (2004) (respectively: $S>0.33$ and $C\geq0.5$). The different functional trait characteristics and indicator values were used to calculate specific species richness and cumulative weighted cover of these subsets for each individual plot in each survey.

The total basal area (BA) of *Fagus, Quercus, Populus* and other present tree species was calculated and used to calculate the percentage that each tree species makes up of this total.

Tree species were given indices of Shade-Casting Availability (SCA) and Litter Quality (LQ). SCA increases from 1 (low) to 6 (high) and were derived from Baeten et al. (2009). LQ increases from 1 (low) to 5 (high) and were derived from Hermy (1985). SCA and LQ of each plot were calculated as the weighted average of the main tree species and their relative share in BA.

3.2 Non-temporal analyses

3.2.1 Predictive model for rooting intensity based on environmental and plot-level functional trait variables

We constructed a predictive model for determining which environmental and plot-level functional trait variables explain wild boar rooting intensity. Table 2 gives a summary of all available variables tested in this model.

Table 2: Overview response and explanatory variables used to construct the predictive model

Response variable	Explanatory variables				
Number of rooting tracks	Coverage understory	Number AWS	Sand fraction	% Shrub	BA Fagus
	Species richness	Relative % ancient woodland species	Loam fraction	% Tree	BA Quercus
	True Shannon diversity	Number stress tolerant species	Clay fraction	Shade casting index	BA Populus
	Inverse Simpson diversity	Number light demanding species	pH CaCl2 value	Litter quality	BA Other
	Eveness	Number competitor species	Kjeldahl N value	Cover shrub + tree	% Fagus BA
	Cover phanerophytes	% Cover stress tolerant	OM Gloeiverlies	Above ground biomass	% Quercus BA
	Cover Geophytes	% Cover light demanding	Plant available Phosphor	Lying dead wood	% Populus BA
	Cover Hemicryptophytes	% Cover competitors	CEC BaCl2	Standing dead	% Other BA
	Cover Therophytes	Mean Ellenberg values plot (L, F, R and N)			
	Cover Chamaephytes	Mean C, S and R value plot			

To get an undisturbed idea of this relationship, wild boar rooting intensity from 2020 was used as the response variable, while explanatory variables from a situation prior to wild boar recolonization were used (survey 1; 2003-2005). An important assumption here is that wild boar tends to re-root the same areas (Falinski, 1986; Goulding, 2003; Groot Bruinderink & Hazebroek, 1996; Sims, 2006). Since we only work with data from the first survey, a dataset with the vernal flora included was used.

In a first step, spatial autocorrelation of rooting intensity was determined. Since rooting intensity was only measured in 2020 this analysis was performed on a dataset which included all plots. First the spatial coordinates were transformed to a spatial object using package “sp” (Pebesma & Bivand, 2005). Spatial autocorrelation of rooting intensity in regards of plot location was then assessed using Moran’s I and Mantel tests (9999 permutations) and visualized as a semivariogram using respectively packages “ape” (Paradis E. & K., 2019), “ade4” (Chessel et al., 2004) and “gstat”(Pebesma, 2004). This was done for the entire dataset and for the forest reserves separately. Final semivariograms were plotted using the “ggplot2” package (Wickham, 2016).

In a next step the distribution of the rooting signs was determined. Since we work with count data (number or rooting signs) only distributions for discrete date were considered. Packages “fitdistrplus” (Delignette-Muller & Dutang, 2015), “logspline” (Kooperberg et al., 2020), “actuar” (Dutang et al., 2008), “pscl” (Jackman et al., 2007) were used to determine, visualize and assess possible distributions. Possible distributions were assessed based on the Akaike Information Criterion (AIC) and vuong tests. Since these analyses suggested a negative binomial distribution, problems with possible overdispersion were directly handled (Ismail & Jemain, 2007). Therefore, in further analyses of wild boar rooting modeling we always worked with the negative binomial distribution.

Explanatory variable selection was done via the Elastic Net method provided by package “glmnet” (Friedman et al., 2010). The advantage of glmnet is that it can work with a negative binomial distribution as family argument by incorporating package “MASS” (Venables & Ripley, 2002). Function glm.nb from “MASS” was used to fit a first exploring negative binomial regression model in order to find the best value for the dispersion parameter of the negative binomial distribution, theta (θ=2.916). Theta can be seen as a measure of overdispersion with respect to a Poisson distribution. When theta reaches infinity a Poisson model is fitted (Hilbe, 2014). Function cv.glmnet was then used to do a cross validation of our glmnet in order to obtain the ideal value for lambda, a regularization parameter that controls the penalty strength of our model (Friedman et al., 2010). This was repeated several times with different values of the mixing parameter alpha in order to find the ideal model parameters for the final Elastic Net (α = 0.35 and Lambda = 1.21235). When alpha is 1, the Elastic Net regression becomes a ridge regression, when alpha is 0, the Elastic Net regression becomes a Lasso regression (Zou & Hastie, 2005). Finally, an Elastic Net Regression with the defined model parameters was carried out. We used the number of rooting signs as response variable and all other variables (see table 2) as explanatory variable for the eventual variable selection.

The resulting variables from previous step were used to construct a predictive generalized additive mixed model (GAMM) for rooting intensity using “mgcv” package (Wood et al., 2016). Function glm.nb from “MASS” was again used to fit a first exploring negative binomial regression model in order to find the best value for the dispersion parameter of the negative binomial distribution, theta (θ= 1.550). Then a main effects model with all resulting variables was constructed. A variogram of the residuals was constructed using the Variogram function from package “nlme” (Pinheiro et al., 2017) to check again for spatial autocorrelation. Forest reserve was added as random factor to account for repeated sub samples in the forest reserves and a spatial correlation structure was added to account for spatial autocorrelation. A GAMM model was chosen over a generalized linear mixed model (GLMM) due to the ability to account for spatial autocorrelation and random effects using smooth terms. GAMM are useful for accounting for a non-linear phenomenon, like spatial autocorrelation, that needs to be accounted for but is not directly of interest. The other variables of interest are included as normal generalized linear terms and can be interpreted like in normal GLMM’s (Lyons, 2018).

Significance of the chosen variables were tested with the anova.gam function from package "mgcv" (Wood & Roark, 1980). Using this method, each variable is tested with the Wald test of significance, this is similar to a type III ANOVA method. For visualization, significant variables were then plotted against rooting intensity using the scatterplot function from package "car" (Fox, 2019).

3.2.2 Plant species and plant community composition related analysis considering wild boar preferences

To find a relation between different levels of rooting intensity and specific understory plant species an Indicator Species Analysis (ISA) was done using the multipatt function from package "indicspecies" using 9999 permutations (Cáceres & Legendre, 2009). For this analysis we worked with the categorical variable with rooting classes.

To allow for an objective classification of plots in vegetation types or communities an agglomerative cluster analysis with a Chord distance matrix was done using package "stats" and "vegan" (Oksanen et al., 2013; R Core Team, 2021). The best method (UPGMA) was determined using the cophenetic correlation (0.966) and Gower's index (59.07). The silhouette width and Mantel approach were used to assess the optimal number of clusters (variable and not easy interpretable results).

Next, differences in understory community composition between different levels of rooting intensity was tested for significance using ANOSIM and PERMANOVA using a Chord distance matrix. Tests were performed using the anosim and adonis functions from package "Vegan" (Oksanen et al., 2013) and significance was tested using 9999 permutations. Using the function pairwise.adonis from package "pairwiseAdonis" (Martinez Arbizu, 2017), Post-hoc pairwise multilevel comparison was done when the ANOSIM and PERMANOVA tests revealed significant differences between groups of rooting intensity.

A Nonmetric multidimensional scaling (NMDS) using the Chord Distance matrix was plotted to compare and visualize the results of these tests. This was done using package "vegan" (Oksanen et al., 2013) and plotted with "ggplo2" (Wickham, 2016). The choice of ordination analyses can be based on the length of the first DCA axis (5.9335 S.D.) and the size of the sampled gradient. According to Lepš & Šmilauer (2003) unimodal methods should be used when the length of the first axis > 4, and linear methods when the length < 3. For values >3 and <4 both types are possible. The large gradient sampled and the obtained length of the first DCA axis (5.9335 S.D.) suggest unimodal ordination analyses (DCA and CCA). However, since we have community data with lots of species' absences (zero values) a Chord distance measure instead of using the raw community data can be recommended (Blaud, 2014; Jacquemyn, 2019; Paliy & Shankar, 2016; Ramette, 2007). Therefore, the NMDS method was chosen since DCA works on the raw data. Rooting intensity and plant species significantly ($p<0.01$) contributing to the plot ordination were post-hoc plotted.

Since the plots measured in either Everzwijnbad or Pruikenmakers are in fact pseudoreplicates instead of true independent replicates, also differences in understory composition between the two forest reserves was tested using ANOSIM and PERMANOVA tests. When there were significant differences, the ANOSIM and PERMANOVA tests for the effect of rooting category on plant communities were repeated on separate subsets of the data containing either data from Everzwijnbad or Pruikenmakers. Also here, post-hoc pairwise PERMANOVA multilevel comparison was done when the ANOSIM and PERMANOVA tests revealed significant differences between rooting categories. These results were again visualized with an NMDS using a Chord distance measure.

3.3 Temporal analysis

The temporal analysis was used to compare three snapshots. Survey 1 represents a situation where wild boar is still absent, survey 2 represents a situation where wild boar has returned but is still a low population density and survey 3 represents a situation with increased wild boar population density.

Using the “mgcv” and “stats” package (R Core Team, 2021; Wood et al., 2016) Wald tests within a generalized additive mixed model (GAMM) framework were used to test for significant differences in species cover between the surveys (α=0.05). Forest reserve and plot ID were added as random factors to account for repeated sub samples in the forest reserves and repeated measures between the surveys. A spatial correlation structure was added to account for spatial autocorrelation. If statistically significant results were obtained, pairwise post-hoc tests using Bonferroni corrections (α =0.017) were carried out to explore significance in species cover between different surveys.

The same method was used to test for significant differences in total percentage herbaceaous understory cover, species richness, diversity indices (Shannon, Simpson and Eveness) and plot level species functional traits (lifeforms (Raunkiaer, 1934), AWS (Hermy et al., 1999), CSR strategy (Grime, 1979; Hunt et al., 2004) and Ellenberg value for light ((Ellenberg et al., 2001; Hill et al., 1999) between the surveys. Again, if statistically significant results were obtained, pairwise post-hoc tests using Bonferroni corrections (α =0.017) were carried out.

An Indicator Species Analysis (ISA) with 9999 permutations was carried out to find indicator species for each survey with increasing wild boar disturbance using he multipatt function from package “indicspecies” (Cáceres & Legendre, 2009).

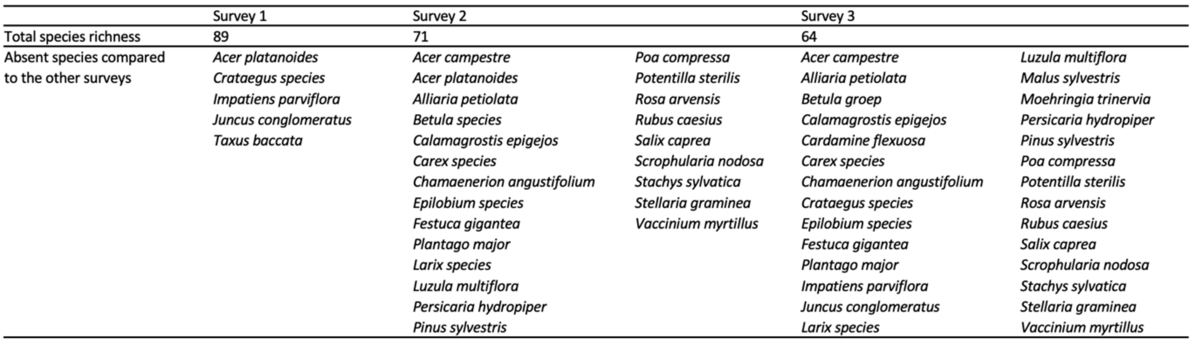
For the temporal part, also an agglomerative cluster analysis with a Chord distance matrix was done using package “stats” and “vegan” (Oksanen et al., 2013; R Core Team, 2021). This allows for an objective classification of plots in vegetation types or communities. The best method (UPGMA) was determined using the cophenetic correlation (0.746) and Gower’s index (1133.44). The silhouette width and Mantel approach were used to assess the optimal number of clusters (again variable and not easy interpretable results). Finally, differences in understory community composition between the surveys was tested for significance using ANOSIM and PERMANOVA using a Chord distance matrix. Tests were performed using the anosim and adonis functions from package “Vegan” (Oksanen et al., 2013) and significance was tested using 9999 permutations. A Nonmetric multidimensional scaling (NMDS) using the Chord Distance matrix was plotted to compare and visualize the results of these tests. This was done using package “vegan” (Oksanen et al., 2013) and plotted with “ggplo2” (Wickham, 2016). We again chose for NMDS with a Chord distance measure, due to the same reasons as mentioned above. Also differences in understory composition between the two forest reserves was tested. When there was significant difference the ANOSIM and PERMANOVA tests were repeated on separate subsets of the data containing either data from Everzwijnbad or Pruikenmakers. These results were again visualized with an NMDS using a Chord distance measure. Using the function pairwise.adonis from package “pairwiseAdonis” (Martinez Arbizu, 2017), Post-hoc pairwise PERMANOVA multilevel comparison was done when the ANOSIM and PERMANOVA tests revealed significant differences between surveys.

If wild boar rooting exerts impacts on the herbaceous plant community and re-rooting in the same plots does occur (Falinski, 1986; Goulding, 2003; Groot Bruinderink & Hazebroek, 1996; Sims, 2006), increasing differentiation in understory plant community composition can be expected between the plots with different levels of rooting intensity through the years. This was also tested using ANOSIM and PERMANOVA tests with a Chord distance matrix. Tests were repeated for each survey with the categorical variable for rooting intensity as a factor for grouping the observations. Significance difference between forest reserves for each survey was also examined. If these results were significant, the tests were repeated for each forest reserve separately. ANOSIM and PERMANOVA tests were performed using the anosim and adonis functions from package “Vegan” (Oksanen et al., 2013) and significance was tested using 9999 permutations.

Results

In general, a decline in total species richness between the different surveys was recorded. In 2003-2005 (survey 1) total species richness was 89, in 2013-2015 (survey 2) species richness declined to 71 and in 2020 (survey 3) total species richness further declined to 64. Table 3 gives a summary of which species were absent in each survey compared to the other surveys.

Table 3: Total species richness and species that were not present surveys in comparison to the other surveys



	Survey 1	Survey 2		Survey 3	
Total species richness	89	71		64	
Absent species compared to the other surveys	*Acer platanoides*	*Acer campestre*	*Poa compressa*	*Acer campestre*	*Luzula multiflora*
	Crataegus species	*Acer platanoides*	*Potentilla sterilis*	*Alliaria petiolata*	*Malus sylvestris*
	Impatiens parviflora	*Alliaria petiolata*	*Rosa arvensis*	*Betula groep*	*Moehringia trinervia*
	Juncus conglomeratus	*Betula species*	*Rubus caesius*	*Calamagrostis epigejos*	*Persicaria hydropiper*
	Taxus baccata	*Calamagrostis epigejos*	*Salix caprea*	*Cardamine flexuosa*	*Pinus sylvestris*
		Carex species	*Scrophularia nodosa*	*Carex species*	*Poa compressa*
		Chamaenerion angustifolium	*Stachys sylvatica*	*Chamaenerion angustifolium*	*Potentilla sterilis*
		Epilobium species	*Stellaria graminea*	*Crataegus species*	*Rosa arvensis*
		Festuca gigantea	*Vaccinium myrtillus*	*Epilobium species*	*Rubus caesius*
		Plantago major		*Festuca gigantea*	*Salix caprea*
		Larix species		*Plantago major*	*Scrophularia nodosa*
		Luzula multiflora		*Impatiens parviflora*	*Stachys sylvatica*
		Persicaria hydropiper		*Juncus conglomeratus*	*Stellaria graminea*
		Pinus sylvestris		*Larix species*	*Vaccinium myrtillus*

1. Non-temporal analysis

1.1 Predictive model for rooting intensity based on environmental and plot-level functional trait variables

1.1.1 Spatial distribution wild boar rooting tracks

Overall, in 114 16 by 16 m plots the number of rooting signs were counted in 2020. The number of rooting tracks varied between 0 and 138 counted signs. 6 plots had 0 rooting tracks (all located in Everzwijnbad) and only two plots had more than 100 rooting tracks (108 and 138). 84 out of 114 plots had no more than 20 counted rooting tracks. After the removal of plots for which no data from the first two surveys was available, we ended up with 101 plots. These plots were used to construct 4 different categories of rooting intensity based on the quantiles. Four groups of more or less equal size were formed: None/Very low rooting (n = 25, 0-6 signs), Low rooting (n = 24, 6-11 signs), Moderate rooting (n = 26, 12-25 signs) and High rooting intensity (n = 26, 26-138 signs). However, for the determination of the spatial distribution of the rooting signs we worked with all 114 plots measured in 2020. For further analysis datasets containing 101 plots were used.

In a first step, spatial autocorrelation of the distribution of wild boar rooting tracks was examined. Figure 30 gives the semivariogram and results of the Moran's I and Mantel test of spatial autocorrelation for the combination of both forest reserves. We saw a clear decrease in semivariance with increasing distance. However, spatial autocorrelation was marginally not significant according to the Moran’s I test and not significant according to the Mantel test.

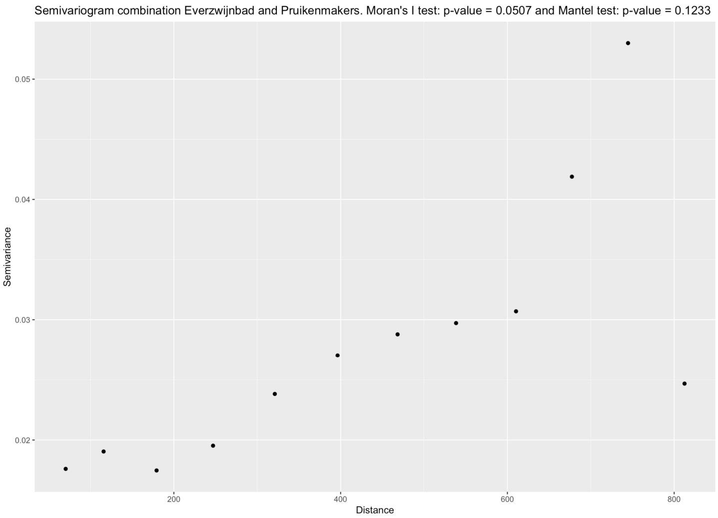


Figure 30: Semivariogram of the number of rooting tracks for the combination of both forest reserves (Everzwijnbad and Pruikenmakers) with obtained p-values of the Moran’s I test and Mantel test.

Figure 31.1 gives the spatial distribution of the vegetation plots in Everzwijnbad expressed as rooting intensity. Larger circles indicated plots with higher number of rooting tracks. Figure 31.2 gives the semivariogram and results of the Moran’s I and Mantel test of spatial autocorrelation for Everzwijnbad. These figures did not show clear spatial patterns in wild boar rooting intensity. Moran’s I and Mantel test were not significant as well.

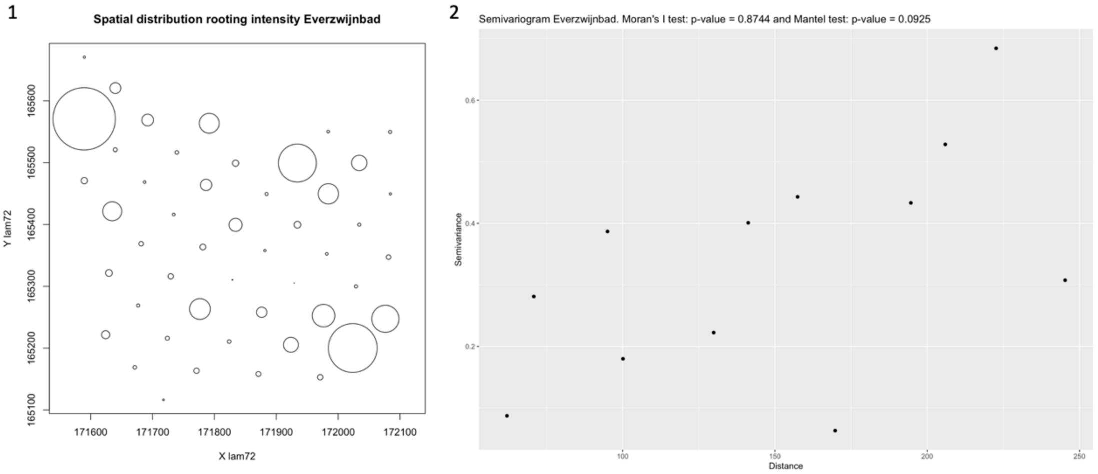


Figure 31: 1) Spatial distribution plots with counted number of rooting tracks in Everzwijnbad, size of plotted circles increases with increasing number wild boar rooting tracks. 2) Semivariogram of the number of rooting tracks for forest reserve Everzwijnbad with obtained p-values of the Moran's I test and Mantel test.

Figure 32.1 gives the spatial distribution of the plots in Everzwijnbad, again, larger circles indicated plots with higher counted number of rooting tracks. Red dots indicated zero rooting counts. Figure 32.2 gives the semivariogram and results of the Moran's I and Mantel test of spatial autocorrelation of the rooting tracks for Everzwijnbad. A pattern in spatial distribution for the number of rooting tracks can be seen. Plots located in the north had rooting tracks. Plots with no rooting tracks were all located at the western border of the forest reserve. The semivariogram and significant results of the Moran's I and Mantel rest confirmed this visual pattern. Plots located closer together had a smaller semivariance than plots further apart, and thus are more similar in number of rooting tracks.

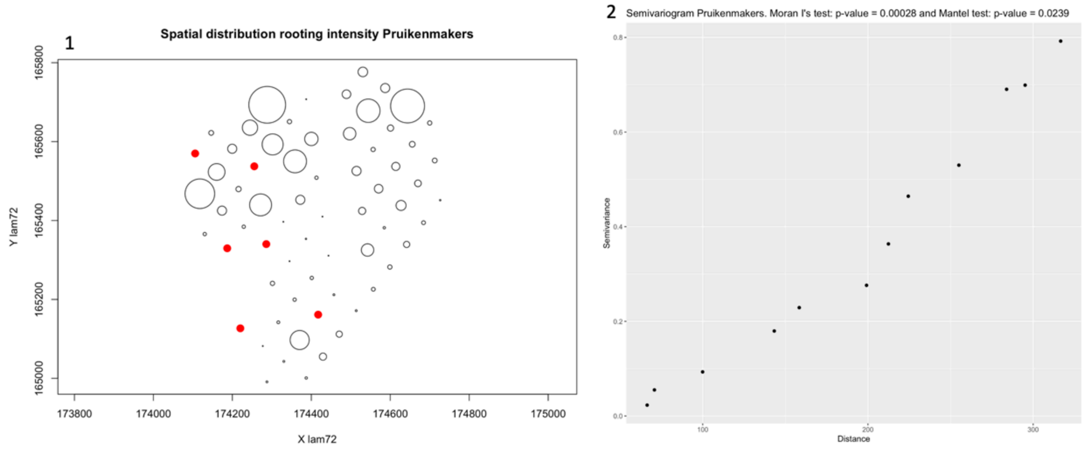


Figure 32: 1) Spatial distribution plots with counted number of rooting tracks in Pruikenmakers, size of plotted circles increases with increasing number of wild boar rooting tracks. Plots with no rooting tracks are indicated with a red dot. 2) Semivariogram of the number of rooting tracks for forest reserve Everzwijnbad with obtained p-values of the Moran's I test and Mantel test.

1.1.2 Variable selection and resulting predictive model

The Elastic Net variable selection retained in first instance 6 variables: cumulative weighted cover chamaephytes, relative number of ancient woodland species, above ground biomass, percentage beech of the total basal area, percentage other trees of total the basal area and loam fraction. Since the glmnet function could not handle missing values and plot 131 in Everzwijnbad had no measurement of plant available P, this variable was not included in the Elastic Net variable selection. Therefore, we constructed two final GAMM's, one where we added plant available P as an extra explanatory variable and one without this extra variable. Based on the AIC (779.582 with plant available P, 786.9878 without) and the R^2 (0.186 with, 0.172 without) we assessed these models and picked the one with the extra term as final model. Table 4 gives the results of the approximate hypothesis tests of this final model. Results of the Wald tests of the significance of each parametric term are given. Relative amount of ancient woodland species, above ground biomass and loam fraction were significant terms for explaining wild boar rooting intensity.

Table 4: Results final GAMM using the most important explanatory variables according to the Elastic Net variable selection. Estimates and standard error of the selection gradients are given together with the results of the Wald test and accompanying significant values (α<0.05), a term to account for spatial autocorrelation and a term to account for repeated subsamples in the same forest reserve were included in the GAMM.

Parametric coefficients	Estimate	Std. Error	t-value	p-value
(Intercept)	3.5073486	1.1732543	2.989	0.003628
Relative cover chamaephytes	1.3457293	1.3673245	0.984	0.327726
Relative amount AWS	4.0627546	1.0948671	3.711	0.000362
Above ground biomass	-0.0016226	0.0006799	-2.387	0.019156
% Fagus of BA	-0.0068223	0.0041086	-1.660	0.100394
% other trees of BA	0.0068625	0.0055417	1.238	0.218901
Loam fraction	-0.0360717	0.0153741	-2.346	0.021220
Plant available P	-0.0032797	0.0047333	-0.693	0.490210

Scatterplots of the number of wild boar rooting tracks in function of the significant terms were made to visualize these relations (figure 33). Also, the relation between the number of wild boar rooting tracks and percentage beech of the total basal area was plotted (p-value = 0.100394). Boxplots of the variables were added at the axes and a regression trend line was drawn (full line). Smooth lines (dotted lines), representing non-parametric estimates of the mean and nonparametric estimates of the conditional variance are plotted as well. These lines are plotted in an attempt to show the non-random, nonlinear association between the variables. This method can allow to make predictions of the response based on the explanatory variable (NetMBA, n.d.). The scatterplot of the number of ancient woodland species suggests a positive trend, plots with the lowest amount of ancient woodland species have the lowest number of tracks. Scatterplots of loam fraction and total above ground biomass suggest negative relationships. On areas with loam fractions > 70%, the maximum amount of counted rooting signs was 20. While plots with <70% loam fractions had a larger variability in counted rooting tracks, here plots with counted rooting signs exceeding 20 are frequent. The relation for above ground biomass was less clear, but in general the most intensely rooted areas were measured in plots with lower amount of total above ground biomass. The scatterplot of % beech of the total BA showed that high % of beech in general had low numbers of counted rooting signs. On the other hand, plots with low % of beach showed a great variability in number of rooting signs.

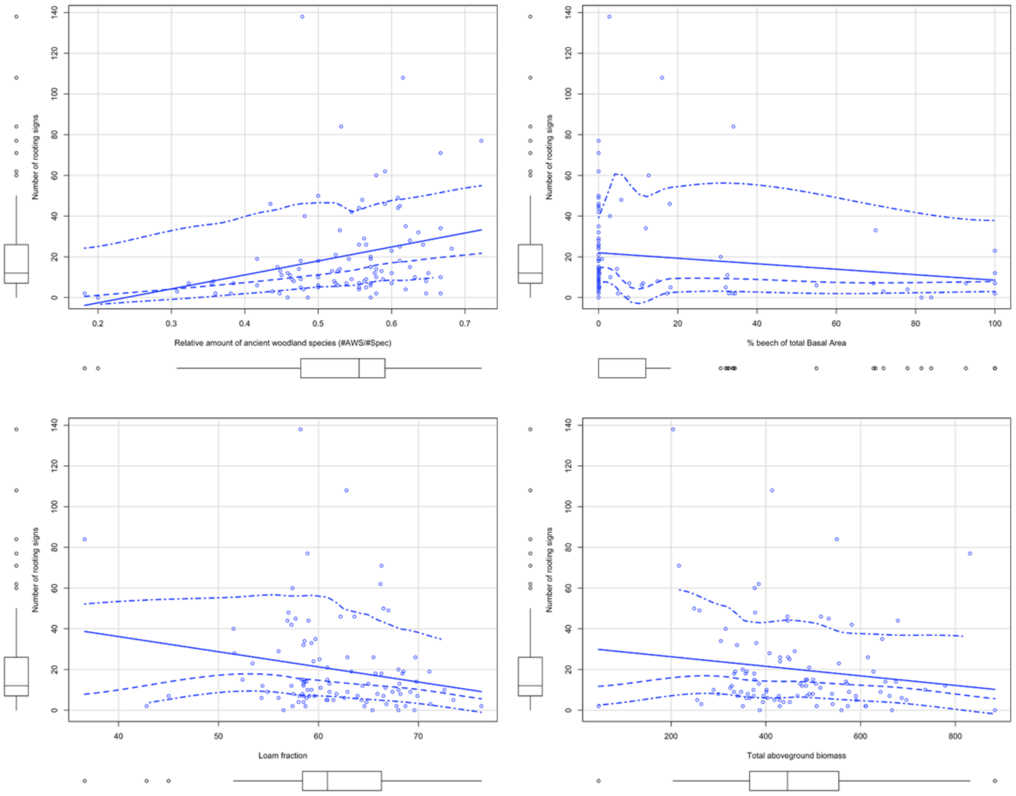


Figure 33: Scatterplots of significant terms explaining wild boar rooting intensity. Relative amount of ancient woodland species, percentage amount of beech trees of total basal area, loam fraction and total aboveground biomass are plotted against number of rooting tracks. Marginal boxplots, regression lines and smooth lines are included.

1.2 Plant species and plant community composition related analysis considering wild boar preferences

Table 5 gives the result of the indicator species analysis of survey 1 between different rooting intensity categories (None/Very low, Low, Moderate and High). The ISA revealed *Frangula alnus* as indicator species for none/very low rooting areas. *Hedera helix* is an indicator species for plots with low rooting intensity and *Oxalis acetosella* for moderate rooting intensities.

Table 5: Indicator species for different levels of rooting intensity. P-values were calculated using 9999 permutations

Indicator species analysis survey 1		
Species	Rooting intensity	p-value
Frangula alnus	None/very low	0.019
Hedera helix	Low	0.0387
Oxalis acetosella	Moderate	0.0488

Figure 34 shows the results of the agglomerative clustering to allow for an objective classification of plots in community or vegetation types. Analysis suggesting the optimal number of clusters were however strongly variable (fusion plot suggested 6-7, silhouette width approach suggested 13 and Mantel approach suggested 19 plots). Therefore, the final dendrogram is given without statistically computed unique groups. The dendrogram, however, did suggest differences in vegetation types between plots in Everzwijnbad (blue square) and Pruikenmakers (red square), these squares were added manually based visual inspection.

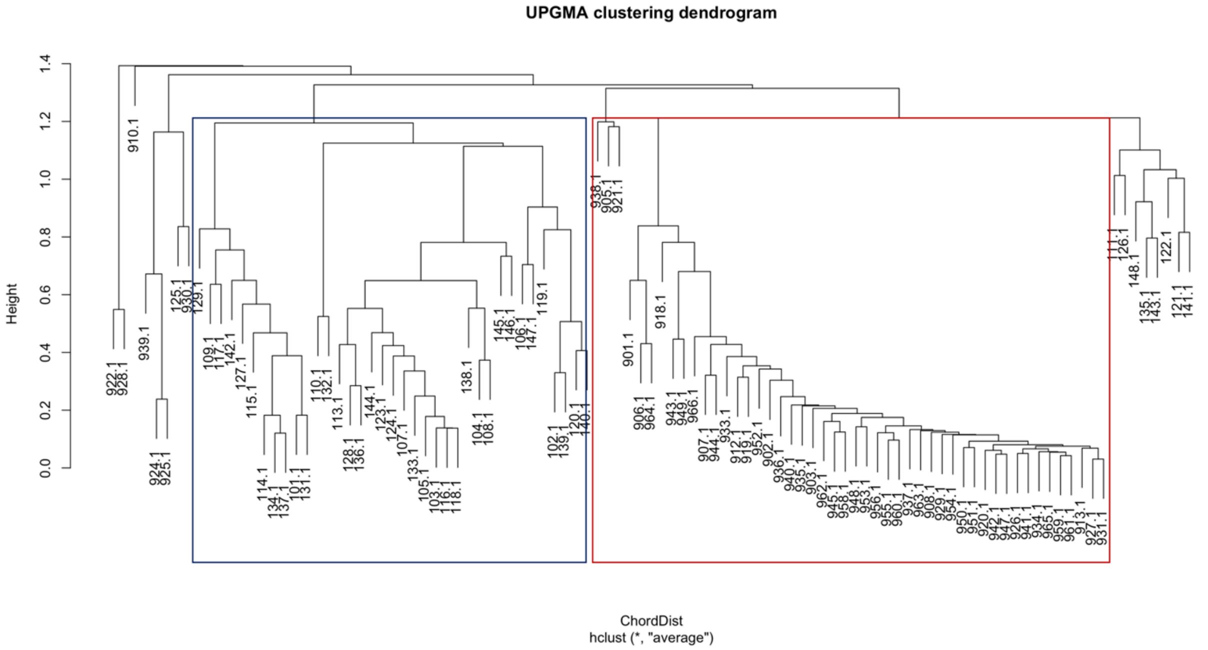


Figure 34: Obtained cluster dendrogram from survey 1 (average/UPGMA method) of the Chord distance matrix. Blue square contains only plots from Everzwijnbad, red square contains only plots form Pruikenmakers

ANOSIM and PERMANOVA tests revealed no significant differences in understory composition between the different levels of rooting intensities in the first survey. However, as suggested by the dendrogram above, significant difference in understory composition was detected between the two forest reserves (table 6). These results were visualized using a NMDS ordination biplot from the first survey (figure 35). This ordination included all measured plots from both forest reserves. Rooting intensity was included as an environmental variable and significant species (α<0.01) contributing to the plot ordination were plotted as vectors as for interpretation of the results. The figure shows a clear distinction between the different forest reserves, plots of Everzwijnbad were clustered on the left side and plots of Pruikenmakers are clustered on the right side. Different levels of rooting intensity were shown in different colors, no clear clustering could be seen in terms of rooting intensity. These results are in line with the ANOSIM and PERMANOVA results (table 6).

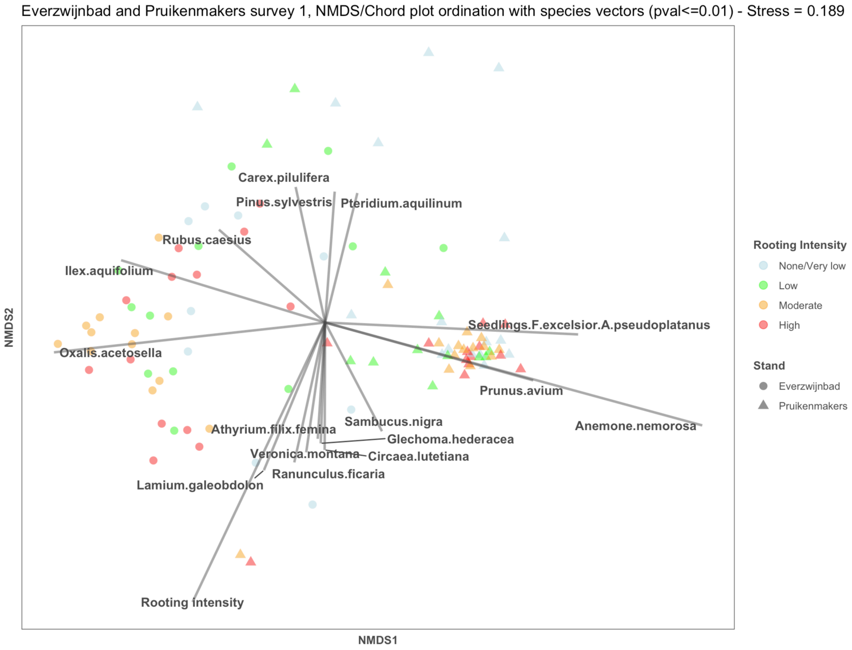


Figure 35: Two-dimensional biplot plot ordination obtained from NMDS ordination based on Chord distance measure calculated from species abundance values from Everzwijnbad and Pruikenmakers during the first survey. Circles represent Everzwijnbad, triangles represent Pruikenmakers. Color code represent rooting intensity. Vectors of rooting intensity and plant species significantly (α<0.01) contributing to the plot ordination are post-hoc added

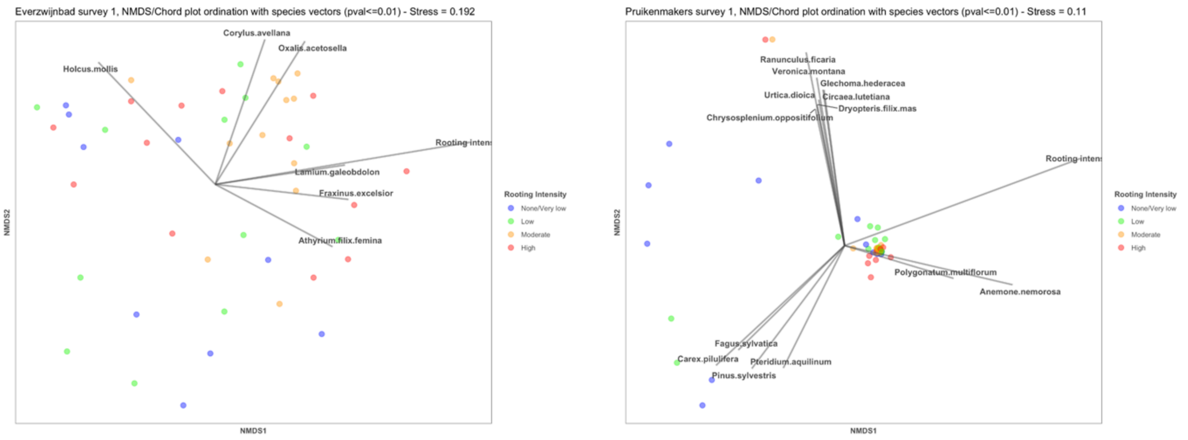
Since figures 34 and 35 and the results of the ANOSIM and PERMANOVA tests between the forest reserves (table 6) suggested difference in understory composition between both forest reserves, these analyses were repeated for each reserve separately. ANOSIM and PERMANOVA tests revealed significant differences in understory composition between the different levels of rooting intensities in Everzwijnbad but no clear significance in Pruikenmakers (non-significant ANOSIM test and slight significant PERMANOVA test (table 6)).

Table 6: Summarizing table with various test statistics and p-values obtained through ANOSIM and PERMANOVA tests. First significant difference in plant understory composition between plots with different classes of rooting intensity is tested for the entire survey 1 (Everzwijnbad and Pruikenmakers together). Then significant difference

between both forest reserves was tested. And finally significant difference between different classes of rooting intensity is tested for Everzwijnbad and Pruikenmakers separately.

	Test statistc	p-values
Tests for significance differences between rooting intensities in both reserves		
ANOSIM	0.01272	0.1825
PERMANOVA	1.3362	0.1657
Test for significance difference between forest stands		
ANOSIM	0.5609	<0.001
PERMANOVA	41.454	0.001
Test for significance differences between rooting intensities in Everzwijnbad		
ANOSIM	0.1344	0.0028
PERMANOVA	2.201	0.0039
Test for significance differences between rooting intensities in Pruikenmakers		
ANOSIM	0.02269	0.1469
PERMANOVA	1.7579	0.0434

These results were again visualized using a NMDS ordination biplot from the first survey, but this time for each forest reserve separately (figure 36). Also here, rooting intensity was included as an environmental variable and significant species (α<0.01) contributing to the plot ordination were plotted as vectors for interpretation of the results. Plots with high and moderate rooting intensities were more copious on the top part of the biplot from Everzwijnbad, while plots with none/very low rooting intensity were clustered on the below/left part. However, clear separation in different understory pant communities between rooting intensities are not visually present. Visualization of the results for Pruikenmakers (figure 36, right side) showed no clear separation of plots with different levels of rooting intensity. This visualization was in line with the non-significant results of the ANOSIM test.



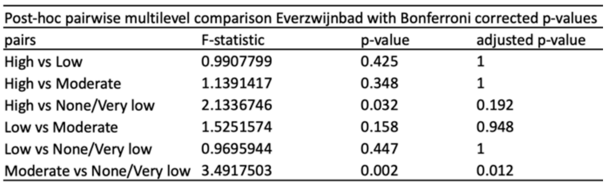
Everzwijnbad survey 1, NMDS/Chord plot ordination with species vectors (pval<=0.01) - Stress = 0.192

Pruikenmakers survey 1, NMDS/Chord plot ordination with species vectors (pval<=0.01) - Stress = 0.11

Figure 36: Two-dimensional biplot plot ordination obtained from NMDS ordination based on Chord distance measure calculated from species abundance values from respectively Everzwijnbad (left) and Pruikenmakers (right) during the first survey. Color code represent rooting intensity. Vectors of rooting intensity and plant species significantly (α<0.01) contributing to the plot ordination are post-hoc added

Since ANOSIM and PERMANOVA results indicated significant differences in understory composition between the different levels of rooting intensities in Everzwijnbad, post-hoc multilevel PERMANOVA comparison between pairwise combinations of rooting intensities was done for Everzwijnbad (table 7). A significant difference in understory plant composition between the none/very low rooting intensity group and moderate rooting intensity group was found, these results were in line with the trend visual on the plot ordination for Everzwijnbad (figure 36 left side). P-values were Bonferroni corrected to correct for multiple comparisons.

Table 7: Post-hoc PERMANOVA multilevel comparison tests to test for significance between pairwise combinations of rooting classes for Everzwijnbad using. P-values were Bonferroni corrected to account for multiple testing.

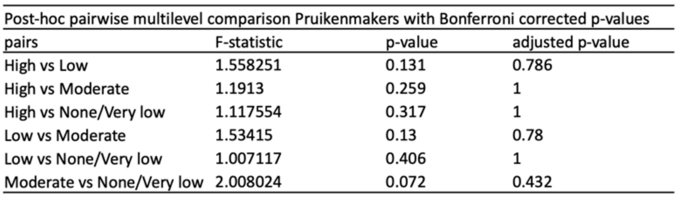


Post-hoc pairwise multilevel comparison Everzwijnbad with Bonferroni corrected p-values

pairs	F-statistic	p-value	adjusted p-value
High vs Low	0.9907799	0.425	1
High vs Moderate	1.1391417	0.348	1
High vs None/Very low	2.1336746	0.032	0.192
Low vs Moderate	1.5251574	0.158	0.948
Low vs None/Very low	0.9695944	0.447	1
Moderate vs None/Very low	3.4917503	0.002	0.012

The ANOSIM test for Pruikenmakers indicated no significant difference between rooting intensity groups while the PERMANOVA test revealed slight significance (table 6). Post-hoc multilevel PERMANOVA comparison between pairwise combinations of rooting intensity groups for Pruikenmakers confirmed these results (table 8). No pairwise significance was found. P-values were again Bonferroni corrected to correct for multiple comparisons.

Table 8: Post-hoc multilevel comparison tests to test for significance between pairwise combinations of rooting classes for Pruikenmakers. P-values were Bonferroni corrected to account for multiple testing.



Post-hoc pairwise multilevel comparison Pruikenmakers with Bonferroni corrected p-values

pairs	F-statistic	p-value	adjusted p-value
High vs Low	1.558251	0.131	0.786
High vs Moderate	1.1913	0.259	1
High vs None/Very low	1.117554	0.317	1
Low vs Moderate	1.53415	0.13	0.78
Low vs None/Very low	1.007117	0.406	1
Moderate vs None/Very low	2.008024	0.072	0.432

2 Temporal analysis

2.1 Changes on individual plant level and plot-level functional traits

Table 9 gives mean characteristic cover (excluding plots with species absence) and number of observations of all plant species in the understory that had a significant change in cover through the surveys. In total 23 species significantly increased in cover through the years. 9 species significantly decreased in cover and 8 species had a significant percentage change in cover due to a decrease in number of observations rather than due to decrease in mean cover. Species with significant increasing cover through the surveys were mainly seedlings from tree species and ferns. In general, survey 2 took on an intermediate position in terms of number of observations and mean cover of plant species. Minimum/maximum values of characteristic cover were always found in either survey 1 or 3.

Table 9: Number of observations and mean percentage characteristic cover of plant species in the herbaceous layer for the three surveys calculated in 101 sample plots. P-values are calculated on cover differences between surveys and obtained through Wald tests with corrections for repeated measures through the years, spatial autocorrelation and repeated sub-sampling in the forest reserves. Post-hoc comparisons between pairwise combinations are Bonferroni corrected. Only species with significant changes in cover are included in the table. Table is divided in species with increasing mean cover (left), decreasing mean cover (top-right) and species with significant p-values due to decreasing number of observations rather than mean cover.

Species	Survey 1		Survey 2		Survey 3					Survey 1		Survey 2		Survey 3			
Increasing in cover	#plots	% cover	#plots	% cover	#plots	% cover	p-value	Post-hoc (p<0.017)	Decreasing in cover	#plots	% cover	#plots	% cover	#plots	% cover	p-value	Post-hoc (p<0.017)
Acer pseudoplatanus	94	1.60	91	5.08	101	20.01	<0.001	1vs2, 1vs3, 2vs3	*Alliaria petiolata*	3	0.10	0	0.00	0	0.00	0.0299	only in survey 1
Athyrium filix femina	88	3.49	88	5.93	88	6.32	<0.001	1vs2, 1vs3	*Cardamine flexuosa*	6	0.10	1	0.10	0	0.00	0.00242	1vs3
Carpinus betulus	38	0.15	37	0.23	37	1.77	0.002	1vs3, 2vs3	*Convallaria majalis*	54	1.06	36	0.72	29	0.93	0.0314	none
Castanea sativa	7	0.37	11	0.32	36	0.74	<0.001	1vs3, 2vs3	*Luzula multiflora*	1	0.10	0	0.00	0	0.00	<0.001	1vs2, 1vs3, 2vs3
Corylus avellana	63	0.10	75	0.13	84	2.94	<0.001	1vs3, 2vs3	*Malus sylvestris*	5	0.10	3	0.10	0	0.00	0.000123	1vs3, 2vs3
Dryopteris carthusiana	87	0.73	91	0.79	88	3.84	<0.001	1vs3, 2vs3	*Oxalis acetosella*	85	4.69	84	3.95	85	2.05	0.00221	only in survey 1
Dryopteris dilatata	85	0.46	92	1.81	89	2.75	<0.001	1vs2, 1vs3	*Plantago major*	1	0.10	0	0.00	0	0.00	<0.001	1vs2, 1vs3, 2vs3
Dryopteris filix mas	23	0.27	23	0.52	34	1.61	0.00704	none	*Rubus caesius*	6	0.10	0	0.00	0	0.00	0.00217	1vs2, 1vs3
Fagus sylvatica	72	0.18	94	0.83	97	5.75	<0.001	1vs2, 1vs3, 2vs3	*Scrophularia nodosa*	4	0.10	0	0.00	0	0.00	0.0134	none
Fraxinus excelsior	28	0.10	3	0.10	40	0.51	0.0038	1vs2, 1vs3, 2vs3	Decreasing # of plots	#plots	% cover	#plots	% cover	#plots	% cover	p-value	Post-hoc (p<0.017)
Hedera helix	52	0.43	61	2.33	75	6.53	0.0099	none	*Carex pallescens*	6	0.10	1	0.10	1	0.10	0.02	none
Juncus effusus	17	0.10	4	0.10	4	0.58	0.000846	1vs3, 2vs3	*Carex pilulifera*	11	0.10	4	0.10	3	0.10	0.00283	1vs3
Maianthemum bifolium	20	0.29	10	0.34	6	1.23	0.0119	none	*Galeopsis species*	16	0.10	7	0.10	4	0.10	0.000289	1vs2, 1vs3
Melica uniflora	26	0.87	31	2.89	35	4.75	<0.001	1vs2, 1vs3	*Holcus mollis*	72	5.36	62	4.36	54	4.36	<0.001	1vs3, 2vs3
Milium effusum	91	0.37	90	1.99	89	2.52	0.00218	1vs3	*Luzula pilosa*	67	0.10	40	0.10	22	0.10	0.00391	none
Polygonatum multiflorum	52	0.10	38	0.10	44	0.40	0.00363	1vs2, 1vs3, 2vs3	*Molinia caerulea*	3	0.10	3	0.10	2	0.10	0.00358	2vs3
Populus canescens	12	0.10	12	0.10	15	0.66	0.00346	1vs3, 2vs3	*Quercus rubra*	13	0.10	3	0.10	4	0.10	0.00545	1vs2
Prunus avium	23	0.10	29	0.10	33	0.32	0.0022	1vs3, 2vs3	*Tilia cordata*	13	0.10	4	0.10	7	0.10	0.049	1vs2
Prunus serotina	35	0.15	44	0.15	54	0.90	0.00289	1vs3, 2vs3									
Quercus robur	88	0.46	90	0.65	96	8.30	<0.001	1vs3, 2vs3									
Rubus fruticosus groep	89	0.63	80	0.75	84	5.53	<0.001	1vs3, 2vs3									
Stellaria holostea	30	1.55	30	2.61	32	3.13	0.0254	1vs3									
Taxus baccata	0	0.00	4	0.10	6	0.10	0.00242	1vs3									

Differences between the surveys in total percentage coverage of the understory vegetation, diversity indices and plot-level functional traits were tested for significance using Wald tests (table 10). If surveys differed significantly post-hoc pairwise combinations were tested for significance as well. To correct for multiple testing a Bonferroni corrected significance value (α<0.017) was used to assess significance. Mean values per survey were given for all tested variables. Coverage understory significantly changed between the surveys, also all pairwise combinations were highly significant. Mean total coverage understory increased from 22.5% in survey 1 to 30.9% in survey 2 and 76.6% in survey 3. All diversity indices (species richness, Shannon diversity, inverse Simpson and evenness) were also significant different between the surveys. Mean values decreased first between survey 1 and survey 2 and increased again in survey 3. Except for species richness, the highest mean values were obtained for survey 3. Only species richness was significantly different between all pairwise survey combinations. The other diversity indices, except for evenness, were only significant between survey 2 and 3. Evenness did not show any significant differences between the pairwise combinations.

Number of ancient woodland species significantly decreased between survey 1 and 2 and survey 1 and 3. Plot-level cumulative weighted values of functional signatures scores, based on the CSR-strategy of Grime (1979) and derived using the method of Hunt el al. (2004), also showed significant differences between the surveys. C-score increased while S- and R-score decreased in general. Pairwise post-hoc test indicated significant differences between survey 1 and 3 and 2 and 3. Plot-level cumulative weighted cover of Ellenberg indicator value for light availability of the plots did not change significantly between the surveys.

Cumulative weighted cover of geophytes, hemicryptophytes and therophytes significantly differed between the surveys as well. Calculated mean values per survey were lowest in survey three. Post-hoc test confirmed these observations, comparisons between survey 1 and survey 3 and survey 1 and survey 2 were always significant. The opposite trend was observed for cumulative weighted cover of phanerophytes at plot-level. Post-hoc test revealed a significantly increasing trend between the surveys (1<2<3). These results are in line with the results obtained in table 9, where many three species significantly increased in cover.

Table 10: Mean values of plot-level % coverage understory, species richness, diversity indices, number of ancient woodland species, CSR functional signatures scores, cumulative weighted cover of Ellenberg indicator values and cumulative weighted cover of plant lifeforms for each survey in 101 sample plots. P-values are calculated on differences between surveys and obtained through Wald tests with corrections for repeated measures through the years, spatial autocorrelation and repeated sub-sampling in the forest reserves. Post-hoc comparisons between pairwise combinations are significant if p-values<0.017 (Bonferroni corrected significance level).

	Survey 1	Survey 2	Survey 3		1vs2	1vs3	2vs3
		Mean values		p-value (0.05)	p-value (0.017)	p-value (0.017)	p-value (0.017)
Coverage understory (%)	22.45941	30.91584	76.57228	<0.001	<0.001	<0.001	<0.001
Species richness	19.54455	17.40594	18.23762	0.00121	<0.001	0.00549	0.00113
true Shannon diversity	6.521686	6.238011	7.34691	0.0209	n.s.	n.s.	0.000413
Simpson	4.682352	4.768309	5.462676	0.0192	n.s.	n.s.	n.s. (0.019)
Eveness	2.252928	2.236266	2.551018	0.0138	n.s.	n.s.	0.00295
Number of AWS	9.653465	8.663366	8.742574	<0.001	<0.001	<0.001	n.s.
Mean C-score	0.4532924	0.4765023	0.5397656	<0.001	n.s. (0.0172)	<0.001	<0.001
Mean S-score	0.4436719	0.435516	0.4095852	<0.001	n.s.	<0.001	<0.001
Mean R-score	0.1030357	0.08798165	0.05064915	<0.001	0.00103	<0.001	<0.001
Ellenberg light availability (L)	4.55004	4.396924	4.551607	n.s.			
Cover phanerophytes	0.2939203	0.3435962	0.5809853	<0.001	0.00199	<0.001	<0.001
Cover geophytes	0.09274426	0.05780038	0.03177573	<0.001	<0.001	<0.001	<0.001
Cover hemicryptophytes	0.4955311	0.4652155	0.2699278	<0.001	n.s.	<0.001	<0.001
Cover therophytes	0.0078724	0.00233121	0.000353035	<0.001	0.00103	<0.001	0.00678
Cover chamaephytes	0.110235	0.1310567	0.1169582	n.s.			

Table 11 gives the result of the indicator species analysis between the different surveys. The ISA revealed 9 indicator species for survey 1 and 20 indicator species for survey 3. No indicator species for survey 2 were found. Indicator species for survey 3 were mainly tree species.

Table 11: Indicator species for different surveys. P-values were calculated using 9999 permutations

Indicator species for different surveys		p-value			p-value			p-value
Luzula pilosa	Survey 1	0.0001	*Quercus robur*	Survey 3	0.0001	*Fraxinus excelsior*	Survey 3	0.0001
Persicaria hydropiper	Survey 1	0.0038	*Acer pseudoplatanus*	Survey 3	0.0001	*Polygonatum multiflorum*	Survey 3	0.0004
Rubus caesius	Survey 1	0.0041	*Corylus avellana*	Survey 3	0.0001	*Carpinus betulus*	Survey 3	0.0003
Quercus rubra	Survey 1	0.0104	*Dryopteris carthusiana*	Survey 3	0.0001	*Prunus serotina*	Survey 3	0.0002
Galeopsis species	Survey 1	0.0105	*Fagus sylvatica*	Survey 3	0.0001	*Prunus avium*	Survey 3	0.0008
Cardamine flexuosa	Survey 1	0.0192	*Rubus fruticosus groep*	Survey 3	0.0001	*Populus canescens*	Survey 3	0.0026
Moehringia trinervia	Survey 1	0.0215	*Ilex aquifolium*	Survey 3	0.0001	*Castanea sativa*	Survey 3	0.0015
Scrophularia nodosa	Survey 1	0.036	*Hedera helix*	Survey 3	0.0001	*Dryopteris filix mas*	Survey 3	0.0024
Carex pilulifera	Survey 1	0.0343	*Dryopteris dilatata*	Survey 3	0.0001	*Lamium galeobdolon*	Survey 3	0.011
			Milium effusum	Survey 3	0.001	*Melica uniflora*	Survey 3	0.0492

2.2 Changes on plant community composition level

Differences in understory plant community composition between the surveys were tested using ANOSIM and PERMANOVA tests (table 12). Both tests indicated highly significant differences in plant communities between the surveys. Bonferroni corrected post-hoc multilevel PERMANOVA comparison between pairwise combinations of surveys confirmed these results (table 13). All pairwise combinations had significantly different understory plant communities. A NMDS ordination biplot was used to visualize these results (figure 37). Plots from each survey were plotted with a different color. This figure clearly showed grouping of plots from the different surveys. The plot groupings also became more concentrated through the years. Survey 1 and 2 showed a greater spread than survey 3. Also significant species ($\alpha<0.01$) contributing to the plot ordination were plotted as vectors for interpretation of the results. Significant species for survey 3 were mainly tree species while significant species for survey 1 were mainly herbaceous species. Survey 2 showed an intermediate position. To indicate differences between forest reserves, plots from Everzwijnbad were plotted as squares and plots from Pruikenmakers were plotted as circles. Based on this plot, it seemed that differences between forest reserves became less pronounced, however differences between forest stand were still visible.

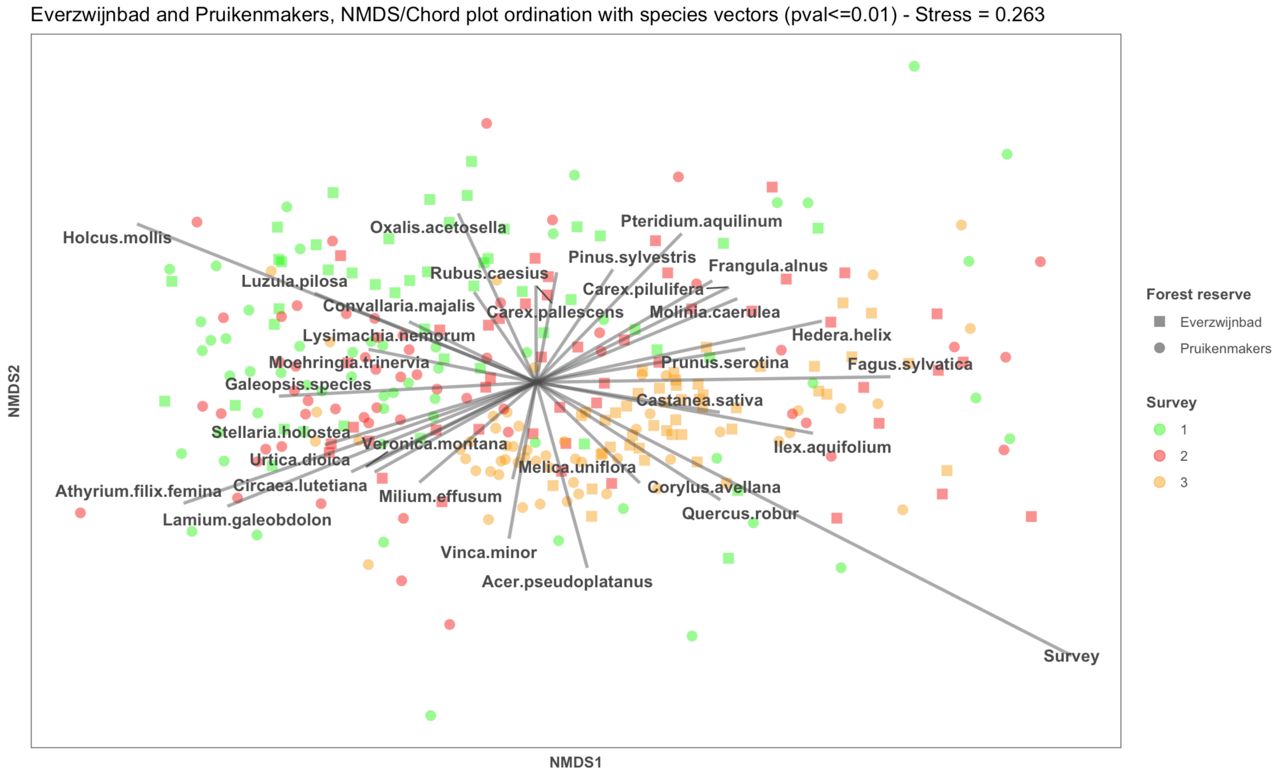


Figure 37: Two-dimensional biplot plot ordination obtained from NMDS ordination based on Chord distance measure calculated from species abundance values from Everzwijnbad and Pruikenmakers for the three surveys. Squares represent Everzwijnbad, circles represent Pruikenmakers. Color code represent different surveys. Vectors of survey and plant species significantly (α<0.01) contributing to the plot ordination are post-hoc added.

Comparison between the forest stands for the entire dataset (3 surveys and both forest reserves) using ANOSIM and PERMANOVA tests confirmed that there were significant differences in understory composition between the forest reserves (table 12). Therefore, the dataset was split up in two subsets, one containing all the data from the 3 surveys of Everzwijnbad and one containig all data from Pruikenmakers. ANOSIM and PERMANOVA tests on these subsets revealed significant differences in community composition between the surveys as well for each forest reserve separately (table 12). Differences in understory plant composition between pairwise combinations of different surveys were tested for both reserves separately using Bonferroni corrected multilevel PERMANOVA pairwise comparisons (table 14). For both forest reserves, each pairwise combination was significantly different in understory plant composition.

Table 12: Summarizing table with various test statistics and p-values obtained through ANOSIM and PERMANOVA tests. First significant difference in plant composition between surveys is tested for the entire dataset (Everzwijnbad and Pruikenmakers together). Then significant difference between both forest reserves was tested. And finally significant difference between surveys is tested for Everzwijnbad and Pruikenmakers separately.

Difference between surveys	Test statistc	p-values
ANOSIM	0.1941	1.00E-04
PERMANOVA	29.732	1.00E-04
Difference between forest stands		
ANOSIM	0.09588	1.00E-04
PERMANOVA	13.694	1.00E-04
Difference between surveys in Everzwijnbad		
ANOSIM	0.2963	1.00E-04
PERMANOVA	26.27	1.00E-04
Difference between surveys in Pruikenmakers		
ANOSIM	0.1645	1.00E-04
PERMANOVA	11.91	1.00E-04

Table 13: Post-hoc multilevel comparison tests to test for significance between pairwise combinations of surveys for the entire dataset. P-values were Bonferroni corrected to account for multiple testing.

Post-hoc comparison between surveys with Bonferroni corrected p-values			
pairs	F-statistic	p-value	adjusted p-value
Survey 1 vs 2	8.16437	0.001	0.003
Survey 1 vs 3	39.56186	0.001	0.003
Survey 2 vs 3	24.39221	0.001	0.003

Table 14: Post-hoc multilevel comparison tests to test for significance between pairwise combinations of surveys for Everzwijnbad (left) and Pruikenmakers (right). P-values were Bonferroni corrected to account for multiple testing.

Post-hoc comparison between surveys in Everzwijnbad with Bonferroni corrected p-values				Post-hoc comparison between surveys in Pruikenmakers with Bonferroni corrected p-values			
pairs	F-statistic	p-value	adjusted p-value	pairs	F-statistic	p-value	adjusted p-value
Survey 1 vs 2	5.720201	0.001	0.003	Survey 1 vs 2	3.519294	0.001	0.003
Survey 1 vs 3	29.32436	0.001	0.003	Survey 1 vs 3	12.43984	0.001	0.003
Survey 2 vs 3	11.188414	0.001	0.003	Survey 2 vs 3	11.688173	0.001	0.003

These significant results were again visualized using a NMDS ordination biplot (figure 38). The left figure shows the visualization for Everzwijnbad and the right figure the visualization for Pruikenmakers. Different surveys were plotted in different colors. These figures show clear differences between the 3 surveys. On both plots, survey 1 showed the greatest spread and survey three the most clear grouping of plots. Significant species (α<0.01) contributing to the plot ordination were plotted as vectors for interpretation of the results. Significant species for survey tree were again mainly tree species. In both forest reserves, survey 2 showed on intermediate position in term of plant understory composition. Different levels of rooting intensity were plotted with a different shape to show possible differences in plant composition between the different levels of rooting intensity for each survey. No clear grouping between different rooting intensities could be visually observed.

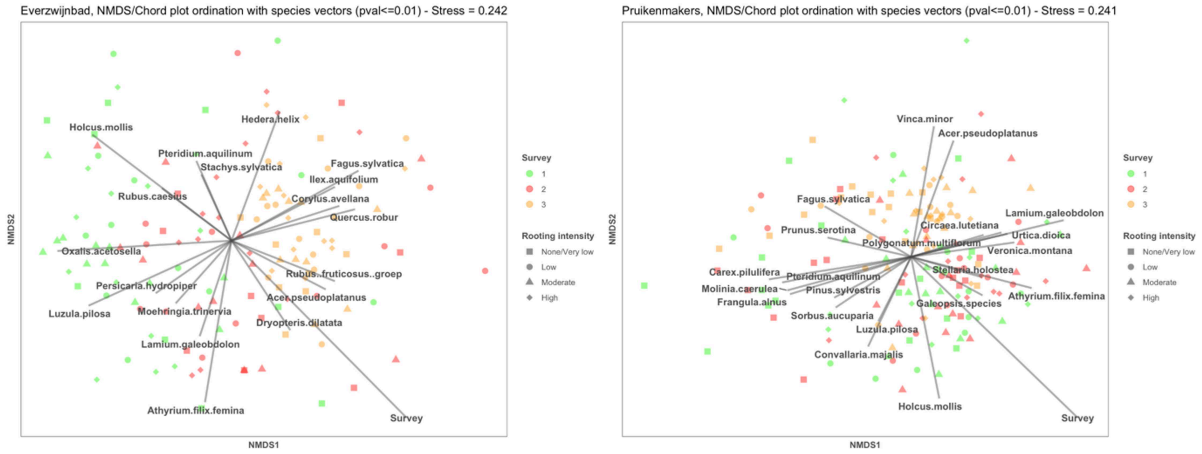


Figure 38: Two-dimensional biplot plot ordination obtained from NMDS ordination based on Chord distance measure calculated from species abundance values from respectively Everzwijnbad (left) and Pruikenmakers (right) for the three surveys. Color code represent survey. Vectors of survey and plant species significantly (α<0.01) contributing to the plot ordination are post-hoc added.

Differences in understory plant composition between the different categories of rooting intensities were tested also for each survey. The results of these ANOSIM and PERMANOVA tests are given in table 15. Since there were also significant differences in understory composition for each survey between both forest reserves, this was always done first for the entire dataset, containing both forest reserves, and then for the forest reserves separately. For the combination of both reserves no significant differences in understory composition was found in any of the surveys. For Everzwijnbad only the first survey showed significant differences in understory composition between the different rooting intensity groups. For Pruikenmakers, only survey 2 had significant differences in understory composition according to the ANOSIM and PERMANOVA test. The ANOSIM test for Pruikenmakers survey three was no longer significant, while the PERMANOVA test was still significant.

Table 15: Summarizing table with various test statistics and p-values obtained through ANOSIM and PERMANOVA tests. Significant difference in plant composition between different rooting intensity categories is tested per survey for the entire dataset (Everzwijnbad and Pruikenmakers together) and for the two forest reserves separately.

Differences between rooting intensity categories per survey for the entire dataset and for Everzwijnbad and Pruikenmakers seperately								
Survey 1	F-statistic	p-value	S1 Everzwijnbad	F-statistic	p-value	S1 Pruikenmakers	F-statistic	p-value
ANOSIM	0.01272	0.1845	ANOSIM	0.1344	0.0033	ANOSIM	0.02269	0.1402
PERMANOVA	1.3362	0.1657	PERMANOVA	2.201	0.0057	PERMANOVA	1.7579	0.0434
Survey 2			S2 Everwijnbad			S2 Pruikenmakers		
ANOSIM	0.01139	0.1945	ANOSIM	-0.01395	0.6188	ANOSIM	0.04804	0.047
PERMANOVA	1.188	0.2166	PERMANOVA	0.83521	0.6891	PERMANOVA	1.6652	0.015
Survey 3			S3 Everwijnbad			S3 Pruikenmakers		
ANOSIM	0.0006531	0.4764	ANOSIM	-0.02737	0.7797	ANOSIM	0.01142	0.2782
PERMANOVA	1.2586	0.1689	PERMANOVA	0.81383	0.7141	PERMANOVA	1.6432	0.0311

Discussion

Rooting intensity

When we compare the wild boar rooting intensity counted in our permanent sample plots with intensities found in previous studies, we can clearly state that wild boar disturbance intensity is not high in our sampled forest reserves. The number of rooting tracks in our 256m^2 plots varied between 0 and 138 counted signs. The majority however (±75%) had no more than 20 rooting signs per plot. Based on the quantiles of the counted rooting signs, the following categories are used: None/Very low rooting (n = 25, 0-6 signs), Low rooting (n = 24, 6-11 signs), Moderate rooting (n = 26, 12-25 signs) and High rooting intensity (n = 26, 26-138 signs).

The study conducted by Brunet et al. (2016) for example classified 1m^2 plots with <25% rooted area as light rooting and plots with >25% rooted area as heavy rooting. Rooted plots used by Sims (2006) were classified as 50cm-50cm plots with no vegetation at all due to rooting at the start of the experiment. And Burrascano et al. (2015), on which we based our rooting sampling, classified heavy rooted macro-areas as areas with a mean of at least 83.92 rooting signs per linear transect of 100-5m. This equals to ±0.18 15cm-wide sign/m^2. The maximum number of rooting signs counted in our study was 138 signs in a plot of 256m^2 (±0.53 15cm-wide sign/m^2). However, the majority had no more than 20 rooting signs per plot (±0.08 15cm-wide sign/m^2). Only two plots with >100 signs were counted. Therefore, we can state that the general impact of wild boar in the sampled forest reserves, Everzwijnbad and Pruikenmakers, is still very low at the moment.

1 Non-temporal analysis

Spatial distribution of wild boar rooting tracks

Analysis on the combination of both forest reserves suggested a marginally non-significant spatial autocorrelation (figure 30). Visually, the semivariogram however does show a trend in wild boar rooting spatial autocorrelation. Plots closer together tend to have a smaller semivariance than plots further apart. The significant results for spatial autocorrelation in Pruikenmakers confirm this trend (figure 32). In this reserve, it is clear that plots in the north are more intensely rooted. Also, all plots with no counted number of rooting signs are found at the western border of the forest reserve. As we can see on figure 29, this western border coincides with the Naamsesteenweg. Therefore, avoidance of these western plots by wild boar due to the presence of this main road can be an explanation for this pattern (D'Amico et al., 2016; Ohashi et al., 2013). The presence of this observed spatial auto-correlation indicates that for the analysis below, predicting the habitat preferences of wild boar rooting intensity, a correction for spatial auto-correlation had to be made.

Predictive model for rooting intensity based on environmental and plot-level functional trait variables

For the construction of the model predicting wild boar rooting intensity based on environmental and plot-level plant functional traits, we worked with rooting intensity data gathered in 2020 and explanatory variables gathered in 2003. This method is chosen to get an idea of the wild boar preferences in an undisturbed forest. However, a big assumption for this method is that wild boar tends to re-root the same areas and avoid other areas through the years (Falinski, 1986; Goulding, 2003; Groot Bruinderink & Hazebroek, 1996; Sims, 2006). However, since no long-term or previous data on rooting distribution is available, the rooting data from 2020 represents only a snapshot measure of the plot subjected to different intensities of wild boar disturbance (Burrascano et al., 2015). Therefore, results from this predictive model must be interpreted with care.

Results of this analysis are given in table 4 and on figure 23. Especially the relative amount of ancient woodland species present in a sample plot seems to positively affect wild boar rooting. This was the only highly significant term explaining wild boar rooting distribution. All plots with more than 20 rooting tracks had at least a relative amount of AWS of 40%. Many of these AWS are geophytes (e.g. *Polygonatum multiflorum, Pteridium aquilinum, Convallaria majalis, Anemone nemorosa, Maianthemum bifolium, Circaea lutetiana, Adoxa moschatellina*) and species with an endochorous dispersion strategy (e.g. *Polygonatum multiflorum, Convallaria majalis, Adoxa moschatellina, Malus sylvestris, Maianthemum bifolium, Corylus avellan, Lonicera periclymenum*). Since rooting for rhizomes, roots, bulbs and tubes and foraging on the ground for fruits and seeds are two main feeding behaviors (Ballari & Barrios-García, 2014; Heptner et al., 1988), a relation between the relative amount of geophytes and endochorous species in rooting intensity can indeed be expected (Baron, 1982; Genov, 1981; Scott & Pelton, 1975).

The significant negative relationships between number of wild boar rooting signs and loam fraction and total above ground biomass are less clear (table 4 and figure 33). The plots show a slight negative trend but points are strongly scattered. Combinations of both low and high counted number of rooting signs with increasing loam fraction and total aboveground biomass are present. A noticeable trend during the fieldwork was that plots in monotypic beech tree stands had in general a low number of counted wild boar tracks. The Elastic Net variable selection also selected the percentage of beech trees of the total basal area as an explanatory variable. However, this variable was not significant (p-value = 0.1004). Nonetheless, the scatterplot of this variable in function of the number of counted rooting signs suggests a negative trend (figure 33). Plots where beech trees counted 0-20% of total BA had both low and high counted number of rooting signs. In plots with higher percentages of beech no more than 40 rooting signs are counted, with the exception of one plot with more than 80 signs. This trend seems controversial, since beechnuts is known to be an important part of wild boars diet (Ballari & Barrios-García, 2014; Goulding et al., 1998; Herrero et al., 2005; Schley & Roper, 2003). However, the presence of secure areas for security and hideouts are also important habitat requirements (Heptner et al., 1988; Keuling et al., 2008a; Tack, 2018). These monotypic beech stands have a very low species diversity in general and are characterized by a poorly developed herb and shrub layer. It is possible that these open forest stands are therefore avoided. Also, the low understory plant diversity directly indicates a lower availability of geophytes and endochorous plant species.

Plant species and understory species community composition related preferences

According to an indicator species analysis, *Frangula alnus* is marked as an indicator species for the none/very low rooting intensity group (table 5). In Everzwijnbad, plots with the presence of *Frangula alnus* (plots 116, 121 and 127) are all located in areas classified as the vegetation type *Pteridium aquilinum-Fagus sylvatica* and *Dryopteris-Fagus sylvatica* sensu Van Mechelen et al. (1997). These poor vegetation types are present in the areas dominated by beech trees. For Pruikenmakers, the presence of *Frangula alnus* (plots 919, 925 and 929) is associated with the Oak-Beech forests, sub-association *Anemone nemorosa* (QSa) type and with the Oak-Birch forest (QB) type (Roelandt, 2004). These forest types are present on the sandy and poorest areas of Puikenmakers. *Oxalis acetosella* is an indicator species for moderate rooting intensity plots. This is a typical species of the dominant vegetation type in Everzwijnbad, *Millium effusum-Oxalis acetosella* (Van Mechelen et al., 1997). The presence of this vegetation type is positively correlated with the presence of native oaks and *Acer pseudoplatanus.* This type is the the "richer" vegetation type in this forest reserve. For Pruikenmakers, *Oxalis actosella* is a typical herbaceous species of the Oak-Hornbeam forest (QC) vegetation type (Roelandt, 2004), the most dominant type for Pruikenmakers. Sensu Cornelis et al. (2009), this type can be mainly classified as Ash-Oak forest with *Millium effusum* and *Oxalis acetosella.* This vegetation type is present on the "richer" loamy parts of this forest reserve. These results from the ISA suggest again the preference of wild boar for more rich soil types with richer plant communities and the avoidance of areas dominated by beech trees.

The preference for understory plant communities was tested through multivariate statistics. For this we compare the plant communities between plots with different levels of rooting intensity. The results of the agglomerative clustering (figure 34), NMDS ordination (figure 35) and ANOSIM and PERMANOVA tests (table 6) indicate a significant difference in understory plant composition between both forest reserves. Therefore, we conducted our analysis always first on the entire dataset to determine the global effect and then on separate subsets containing only data from either Everzwijnbad or Pruikenmakers. To avoid pseudoreplication, good conclusions can only be made on the results of these subsets.

For the combination of both reserves, no significant differences in understory composition are obtained (table 6). The plot ordination biplot (figure 35) is a visual representation of these results, also here no clear grouping of plots with different rooting intensities can be observed. As mentioned above, the significant difference in understory composition between the stands however is clear. According to the NMDS, typical significant species for Everzwijnbad are *Oxalis actosella*, and *Ilex aquifolium*. Typical significant species for Pruikenmakers are *Prunus avium* and *Anemone nemorosa*. For Everzwijnbad, this result is in line with the results of the basic inventory done by Van Mechelen et al. in 1997, they indicated the *Millium effusum-Oxalis acetosella* vegetation type as the dominant one for Everzwijnbad. The significant role of *Ilex aquifolium* in the grouping of the plots from Everzwijnbad is not surprising either. This species is known to be quite present in the shrub layer of this forest reserve (Baeté et al., 2004). On the other hand, Pruikenmakers is characterized by the presence of numerous secondary native tree species, like *Prunus avium* (Meuleman, 2006*)*, explaining the role of this species in the NMDS ordination. And according to the vegetation map of the herbaceous understory vegetation created by De Keersmaeker et al. (2009), the dominant vegetation type in Pruikenmakers has a rich vernal aspect with *Anemone nemorosa, Stellaria holostea, Lamium galeobdolon* and *Athyrium filix-femina*, explaining the significant role of *Anemone nemorosa.*

The ANOSIM and PERMOVA test to examine difference in understory composition in rooting intensity classes for both forest reserves separately indicates only significant differences for Evezwijnbad (table 6). Post-hoc pairwise PERMANOVA tests between each category of rooting intensity for Everzwijnbad indicates only a significant difference in understory vegetation composition between the none/very low and the moderate rooting intensity group (table 7). Figure 36 is a visualization of these results, indeed we can see that the plots with moderate rooting intensity are more abundant at the top half of the NMDS biplot, while the plots with none/very low rooting are more abundant at the low/left side of the biplot. The presence of *Oxalis acetosella* is again an import species for the ordination. In line with the results obtained in the ISA (table 5), it is clear that *Oxalis acetosella* is an important species for grouping the plots with moderate rooting intensity.

Based on the results of the predictive model, the ISA, the PERMANOVA and ANOSIM tests we can state that in our study area, wild boar has a preference for plots with a richer soil and richer plant communities. The dominant tree species on these richer soils are native oak species, with an admixture of *Acer pseudoplatanus*, *Fraxinus excelsior*, *Prunus avium*, *Populus canescens, Carpinus betulus* and *Corylus avellana*. Parts dominated by *Fagus sylvatica* are not preferred. The presence of many ancient woodland species, including *Oxalis acetosella,* seems to positively affect the number of counted wild boar rooting signs.

2 Temporal analysis

General observed changes on forest reserve level

If we compare the three consecutive snapshots, the overall species richness strongly declines (table 3). 18 species were lost between survey 1 and 2 and 25 species were lost between survey 1 and 3. These results confirm the recently published decline in species richness at reserve level found by Vandekerkhove et al. (2021). They examined four recently installed forest reserves on fertile loess soils in Flemish Brabant. Forest reserves Everzwijnbad and Pruikenmakers are two of the four examined strict reserves. For our research, we used the same vegetation relevés as they used, only we added a third survey (2020). Further, we also specifically sampled wild boar rooting intensity, which was not included in their study.

Vandekerkhove et al. (2021) contribute this negative effect on reserve level species richness to the introduced zero-management strategy applied in the last decades in Pruikenmakers and Everzijwnbad. Before, these reserves were managed trough small-scaled harvest interventions leading to frequent soil and canopy disturbances. The effect of this reduced disturbance regime leads to a continued closed canopy. This steers towards a vegetation with lower species richness. They found that species requiring soil disturbance and light-demanding species significantly declined.

The recent recolonization of wild boar and associated disturbances can in theory partly restore or replace this former disturbance regime. Wild boar can increase small scale disturbances and again favoring light-demanding species and soil disturbance requiring species. This has led in previous studies to increased plant biodiversity (Brunet et al., 2016; Groot Bruinderink & Dekker, 2010; Kotanen, 1995; Sims, 2006; Welander, 1995). However, the further decrease in general species richness in survey three suggests that the effects of increased deep shade and reduced disturbances due to the non-intervention strategy are not compensated. Impacts of herbivore pressure are density dependent. The population density, together with the applied management strategy and local biotic and abiotic conditions determines whether herbivore impacts are detrimental or positive (Heckel et al., 2010; Nuttle et al., 2014; Pellerin et al., 2010; Ramirez et al., 2018). This density-dependent impact is in line with the intermediate disturbance hypothesis of Connell (1978). The reduced disturbance regime due to the implemented non-management strategy, together with the small wild boar disturbance intensity observed in our study, leads to a structural uniform and more dense vegetation. The low heterogeneity in both light and habitat conditions leads to decreasing species diversity, confirming similar results found in the past (Boch et al., 2013; Lelli et al., 2019; Lucas et al., 2013; Paillet et al., 2010; Ramirez et al., 2018; Vandekerkhove et al., 2021).

Wild boar related changes on individual plant level

The low overall rooting intensity observed in our study area together with the shift towards a more mesic lowland forest due to the introduced zero-management strategy applied (Vandekerkhove et al., 2021), makes it difficult to assess whether the return of wild boar exerts impacts on the forest. As mentioned in the beginning of the discussion, the observed decline in reserve level species richness between the first two surveys (Vandekerkhove et al., 2021), continues further in the results of the third survey.

Significant differences in mean characteristic cover of plant species in the understory are given in table 9. These are strongly in line with the results of the indicator species analysis and the species that are found to be only present in survey 1 (table 11 and table 3). Especially tree and fern species show significant increases in cover. The results of *Acer pseudoplatanus* are remarkable, its mean cover increased from 1.60% in survey 1 to 5.08% in survey 2 and 20.01% in survey 3. This trend is already mentioned in the monitoring reports for both forest reserves (De Keersmaeker et al., 2005a; De Keersmaeker et al., 2009), *Acer pseudoplatanus* was the most numerous rejuvenating tree species. The same trend was also already found in other forest reserves on loamy soils (Wijnendalebos, Janheideberg and Bos Ter Rijst). The monitoring reports also mention that seedlings of *Quercus robur* and *Corylus avellana* are frequent, while on the other hand seedlings of *Fagus sylvatica* are less abundant (De Keersmaeker et al., 2005a; De Keersmaeker et al., 2009). Our results confirm that frequent rejuvenation of *Acer pseudoplatanus, Quercus robur* and *Corylus avellana* is indeed happening. The number of plots with seedlings of these species and their mean cover has increased strongly through the years. Especially survey 3 has significantly higher mean covers for these species than survey 1 and 2. Our results indicate, however, also a strong significant increase in rejuvenation of *Fagus sylcatica* in the last survey.

Vandekerkhove et al. (2021) also reported that shade tolerant species like *Dryopteris carthusiana, D. dilatata, D. filix mas, Athyrium felix femina, Hedera helix, Melica uniflora* and *Millium effusum* significantly expanded in both cover and frequency in Everzwijnbad and Pruikenmakers in the second survey compared to the situation in survey 1. Our results, confirms that this trend continuous in the most recent survey. The observed decline of typical species for disturbed and bare soils and light demanding/gap phase species like *Carex pallescens, Luzula pilosa, Scropholaria nodosa, Periscaria hydropiper* (only found in survey 1) and *Moehringia trinerva* (only found in survey 1 and 2) and the observed decline of typical shade tolerant species like *Convallaria majalis,* and *Rubus caesius* (only found in survey 1) between the first two surveys (Vandekerkhove et al., 2021), also continuous in survey 3 according our results (table 6). This indicates that the effect of a lower disturbance regime due to the cessation of management interventions is still leading to an increased closed canopy cover, resulting in the development of a herbaceous understory with lower species richness. Species typical for lowland mesic oak and beech forests are still increasing in dominance. In line with the continued trend observed in survey tree, we can say that increased wild boar rooting disturbance through the years is not counterbalancing this decrease in disturbance due to the non-management strategy.

Wild boar related changes on plot-level and plot-level functional traits

Changes in total percentage cover of the understory vegetation, diversity indices and plot-level functional traits are also tested for significance (figure 10). Remarkable is the significant increase in total percentage cover through the years. Mean cover increases from 22.5% in survey 1 to 30.9% in survey 2 and 76.6% in survey 3. These results are contradicting with some other results found in the past showing that wild boar rooting can lead to reduction in plant cover. Even reductions up to 80-95% of herb cover have been documented (Barrios-Garcia & Ballari, 2012; Bialy, 1996; Brunet et al., 2016; Howe et al., 1981; Leaper et al., 1999; Massei & Genov, 2004). A large part of this observed increase in total plant cover can be contributed to the increase in cover of tree seedlings and ferns described above. Again contradicting other results, Massei and Genov (2004) mention for example reductions in the density of seedlings of 1.5-5 times. Other results showed that the increased rooting and consumption of mast and seedlings has led to reduced regeneration of *Fagus sylvatica* and *Quercus sp.* in the past (Groot Bruinderink & Hazebroek, 1996; West et al., 2009). This again indicates that wild boar pressure in our study area is still very low.

The significant decrease in plot-level species richness between survey 1 and 2 and survey 1 and 3 are again in line with the shift to a more species poor mesic forest reported by Vandekerkhove et al. (2021). This reported loss in species richness on plot-level supports the intermediate disturbance theory (Connell, 1978). Previous frequent small-scale disturbance corresponds with intermediate disturbance intensities, leading to a higher species richness in survey 1. Cessation of previous small scale frequent management interventions in combination with still low wild boar rooting disturbances leads to a lower species richness (Boch et al., 2013; Lelli et al., 2019; Paillet et al., 2010; Vandekerkhove et al., 2021). We found also a significant difference in species richness between survey 2 and 3, indicating that species richness again increased at plot level in survey 3. However as mentioned above, general species richness at reserve level further decreased. This slight increase in species richness at plot-level in survey 3 compared to survey 2 might be the result of adaptation to this new disturbance regime, leading to a small recovery in species richness. Post-hoc tests on the Shannon diversity Index, Simpson diversity Index and Evenness indicate that there are only significant differences in Shannon diversity and evenness between survey 2 and 3. The Shannon diversity and evenness is again slightly higher in survey 3. A shift to more homogeneous plots with a more homogenous distribution in abundance can be a possible explanation for this increase in diversity measures.

Plot-level cumulative weighted functional signature scores derived using the method of Hunt et al. (2004) show significant decreases in R-score between all surveys. S-score significantly decreased between survey 1 and 3 and 2 and 3, while C-score significantly increased between survey 1 and 3 and 2 and 3. The reduced disturbance regime can explain the significant decrease in R-score, while the very strong increase in abundance of *Acer pseudoplatanus* (C-score = 0.75) and in lesser amount the strong increases in *Dryopteris sp, Melica uniflora* and *Quercus robur*, which are all relatively strong competitors as well, can explain the significant increase in C-score.

Plot-level cumulative weighted Ellenberg indicator value for light availability did not change significantly. However, due to the continued closed canopy resulting in a deep shade forest, a reduction in L-Ellenberg could be expected. But, as mentioned by Vandekerkhove et al. (2021), average L-value was already low at the first survey. Cumulative weighted cover of phanerophytes significantly increased through the years (table 10). These results are clearly in line with the significant observed increases in tree species seedlings in the ground cover. The significant decreases in cumulative weighted mean values of hemicryptophytes are surprising. For example, *Dryopteris sp., Millium effusum* and *Melica uniflora* all increased significantly in mean cover, contrasting this result.

Wild boar related changes on plant community composition level

The ANOSIM and PERMANOVA tests (table 12) and the NMDS visualization of these results (figure 37) performed to indicate significant differences in understory plant composition between the surveys confirm the previous results of a shift towards a more homogenous and mesic community compositions. These results indicate not only a trend in homogenization of the understory vegetation within one reserve, but also between both forest reserves. In other words, both forest reserves are becoming more similar in terms of understory community composition.

This homogenization is increasing through the years, with the strongest grouping of plots observed in survey 3. Survey 2 clearly takes on an intermediate position, indicating a continuous shift towards a typical vegetation of deep shade, mesic oak and beech forests. These results confirm the results found by Vandekerkhove et al. (2021) and indicate that the communities have become even more homogenous in the third survey included in this survey. Indeed, all pairwise combinations between the surveys have significantly different understory plant communities (table 13). As already indicated by the ISA (table 11) and the univariate statistics comparing individual species abundances between the surveys (table 9), especially the seedlings of several tree species are significantly contributing to the grouping of survey 3. Species typical for survey 1 are *Luzula pilosa, Holcus mollis, Rubus caesius and Urtica dioica,* which are more ruderal and light-demanding species.

As mentioned above, not only a homogenization within each forest reserve was observed, but also both reserves become more similar. However, ANOSIM and PERMANOVA tests on the entire dataset, thus containing the three surveys and all plots from both reserves, comparing the understory composition of both reserves still indicate significant differences (table 12). Therefore, we repeated the previous analyses for each reserve separately (table 12). These confirm that understory composition is significantly different for each forest reserve separately as well. Post-hoc pairwise comparisons show that all pairwise combinations per forest reserves are significant as well (table 14). The visualization of these results (figure 38) are similar with the results for the entire dataset. A clear continuous shift to a vegetation characteristic for a more homogenous, closed-canopy mesic oak and beech forest is occurring.

These NMDS ordinations also show no clear differences between rooting intensity groups (plotted in a different shape). If wild boar impacts are present, it could be suspected that through the years plots with different categories of rooting intensities would become more different in terms of undergrowth plant composition. A condition for this would be that wild boar indeed re-root the same areas regularly and avoid others (Falinski, 1986; Goulding, 2003; Groot Bruinderink & Hazebroek, 1996; Sims, 2006). ANOSIM and PERMANOVA tests confirm that for the entire dataset no differences in understory composition are found between the different rooting groups for none of the three surveys. Tests for Everzwijnbad separately only indicate a difference between rooting groups in the first survey. And tests for Pruikenmakers only indicate a clear significant difference between routing groups in survey 2. Survey 3 indicate for neither of the performed tests a clear significant difference between the different rooting categories. This confirms that, even if there are impacts of increased wild boar related disturbances, these are out ruled by the decrease in disturbance regime due to the cessation of management interventions.

Conclusion and future perspectives

Non-temporal analysis

According to our results, it seems that wild boar habitat use is complex. Wild boar pressure is by no means distributed evenly over the habitat. Certain vegetation types are clearly favored while others are rarely used. These vegetation types thus undergo different intensities of wild boar rooting disturbance. These results are in line with other studies done in the past suggesting complex habitat use (Coughenour, 1991; D'Amico et al., 2016; Putman, 1986; Wallis De Vries, 1996). In our study area, the lowest intensities of wild boar are observed parallel with the Naamsesteenweg, indicating probable road avoidance behavior. Also, the presence of geophytes and fruits and seeds are important variables predicting possible wild boar rooting intensity in our study area. The presence of important food sources like mast trees alone, however, seems to be not enough. Also, possibilities to hide and feel secure could explain wild boar rooting disturbance in our study area (Heptner et al., 1988; Keuling et al., 2008a; Tack, 2018). Therefore, in our study area monotypic beech stands with a poor herb and shrub layer are rarely used.

In our study area, wild boar seems to prefer the richer soil types with richer vegetation types like the *Millium effusum-Oxalis acetosella* (sensu Van Mechelen et al. (1997)) dominant in Everzwijnbad and the Ash-Oak forest type with *Millium effusum* and *Oxalis acetosella* (sensu Cornelis et al. (2009)) in Pruikenmakers. Therefore, it is not clear that wild boar avoids the beech stands due to the absence of possibilities to hide, or due to the presence of poorer soil types associated with these beech stands. Past management practices have led to clear relationships between the dominant tree species and the present soil types (De Keersmaeker et al., 2005a; De Keersmaeker et al., 2009). The richer soils were used for coppice-with-standards with oak trees as standards, while the poorer soils were planted with beech or coniferous trees. Results of this past management are still visible today.

Temporal analysis

At the moment, compared to other studies the intensity of wild boar disturbance in our study is only limited (Brunet et al., 2016; Burrascano et al., 2015; Sims, 2006). This, together with the observed shift to a closed-canopy, mesic lowland oak and beech forest due to the cessation of small-scale management interventions (Vandekerkhove et al., 2021), makes it hard to assess wild boar impacts. This effect of reduced canopy and soil disturbance leads to decreasing species richness and shifts in species functional traits and understory community composition. Possible positive or negative effects, if there are any, of wild boar rooting disturbance cannot be easily delineated from other temporal changes. Our results indicate that the trend towards a more mesic forest observed by Vandekerkhove et al. (2021) between survey 1 and survey 2 is further continued in the most recent survey. A clear gradient can be seen, with survey 2 acting as an intermediate situation.

In theory the presence of wild boar and their associated disturbances could counterbalance this decreased disturbance regime due to the none-intervention management. However, we found no evidence that wild boar related disturbances are high enough to restore or replace this former disturbance regime. Especially the significant increase in total percentage cover of the understory vegetation and the significant increases in cover of tree seedlings suggest that wild boar disturbance is very low. Other studies reported negative effects of wild boar rooting on percentage herbaceous cover and tree regeneration due to rooting and seed predation (Barrios-Garcia & Ballari, 2012; Bialy, 1996; Brunet et al., 2016; Groot Bruinderink & Hazebroek, 1996; Howe et al., 1981; Massei & Genov, 2004; West et al., 2009).

Future perspectives

Our results indicate that there are at the moment no detrimental impacts of wild boar related disturbances. However, it was hard to delineate possible impacts related to wild boar and other temporal shifts or changes related to the understory vegetation.

However, it is known that wild boar populations can increase very rapidly (Barrios-Garcia & Ballari, 2012; Fagiani et al., 2014). And it is proven that wild boar can exert considerable density-dependent impacts on fauna and flora (Nuttle et al., 2014; Ramirez et al., 2018). Therefore, it is also crucial to have reliable estimations of the population densities of these animals (Fagiani et al. 2004). Further research and monitoring of the impacts of wild boar on their environment, together with good estimation of their population density could help in determining possible tipping points when wild boar starts to have detrimental impacts. It is expected that at certain densities shifts towards undesirable states can occur (Ramirez et al., 2018). As suggested by Fagiani et al. (2004), in order for this to work, good and sound developed monitoring protocols are essential for evaluating the impacts of wild boar on plants and animals in (forest) ecosystems.

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